Characterisation of neotropical savanna and seasonally dry forest ecosystems by their modern pollen rain

Huw T. Jones

Doctor of Philosophy
The University of Edinburgh
Submitted: 2009

I declare,

(a) that the thesis has been composed by the candidate, and

(b) that the work is the candidate's own, and

(c) that the work has not been submitted for any other degree or professional qualification.

Signed.....

Huw Jones

Characterisation of neotropical savanna and seasonally dry forest ecosystems by their modern pollen rain

Huw T. Jones

At present there is uncertainty over the response of neotropical ecosystems to the climatic changes of the Quaternary. The majority of vegetation reconstructions from the region are derived from fossil pollen records extracted from lake sediments. However, the interpretation of these records is restricted by limited knowledge of the contemporary relationships between the vegetation and pollen rain of neotropical ecosystems, especially for more open vegetation such as savanna and dry forest. This research aims to improve the interpretation of these records by investigating the relationship between the vegetation and modern pollen rain of different savanna and seasonally dry tropical forest (SDTF) ecosystems in Bolivia using artificial pollen traps and surface lake sediments to analyse the modern pollen rain. Vegetation data is used to identify taxa that are floristically important within the different ecosystems and to allow modern pollen/vegetation ratios to be calculated.

The modern pollen rain from the upland savanna is dominated by Moraceae/Urticaceae (35.1%), Poaceae (29.6%), *Alchornea* (6.1%) and *Cecropia* (4.1%), whilst the seasonally-inundated savanna sites are dominated by Moraceae/Urticaceae (30.7%), Poaceae (19.5%), Cyperaceae (14.0%) and *Cecropia* (7.9%). These two different savanna ecosystems are only slightly differentiated by their modern pollen rain. The main taxa in the modern pollen rain of the upland SDTF are Moraceae/Urticaceae (25.8%), *Cecropia* (10.5%), *Acalypha* (7.6%) and Combretaceae/Melastomataceae (6.7%). Seasonally-inundated SDTF is dominated by *Cecropia* pollen to the extent that it was removed from the pollen sum and the main non-*Cecropia* pollen types are Moraceae/Urticaceae (39.0%), unknown type df 61 (6.4%), Asteraceae (6.3%), *Celtis* (6.0%) and *Physocalymma scaberrimum* (4.9%). These two SDTF ecosystems are well differentiated by their modern pollen rain, implying that they may be defined in fossil pollen records. The modern pollen

rain obtained from the surface lake samples is generally complementary to that obtained from the artificial pollen traps for a given ecosystem. All sites have a high Moraceae/Urticaceae pollen signal due to effective dispersal of this pollen type from areas of evergreen forest in close proximity to the study sites. The savanna sites show lower Poaceae percentages than have been previously reported in the literature by some authors and this raises the possibility than the extent of this ecosystem in the past may have been underestimated. Modern pollen/vegetation ratios show that many key vegetation types are absent/under-represented within the modern pollen rain.

Acknowledgements

Firstly, I would like to thank my supervisor, Dr. Francis E. Mayle at the University of Edinburgh, and my co-supervisors, Dr. James Ratter and Dr. Toby Pennington at the Royal Botanic Gardens Edinburgh, for their assistance and guidance for this research. Thanks also to my advisor, Professor Peter Furley, for helpful suggestions that aided this research.

The artificial pollen traps analysed in this research were collected by Francis Mayle (University of Edinburgh) and William Gosling (Open University, UK) between 1999 and 2001. Thanks to Bronwen Whitney (University of Edinburgh) for providing lake sediment pollen counts from Laguna La Gaiba, William Gosling for providing pollen count data from his study sites at NKMNP and Tim Killeen for providing vegetation plot data through the SALVIAS database.

Fieldwork within Bolivia during the Summer of 2006 was made possible thanks to all at the *Museo de Natural Historia*, Santa Cruz, Bolivia. Particular thanks go to Tim Killeen for logistical support and to Marcelo and Wilma Siles for accommodation and wonderful hospitality in Santa Cruz.

Thanks to all those who offered assistance in the field, namely Michael Burn, Bronwen Whitney and Francis Mayle. Additionally, within the Beni of Bolivia, I am grateful to Mauricio Herrera, Vladimir Fuentes, Douglas Bruckner and "Nancho". Thanks to the residents of the village of Florida, Santa Cruz for support in Noel Kempff Mercado National Park and for helping to relocate the study plots! Many thanks to Ezequeile Chavez (Museo de Natural Historia, Santa Cruz, Bolivia) for aiding with botanical identifications in the field.

Laboratory support and guidance with procedure was provided by Julie Mitchell, Elaine McDonald and Anthony Newton. Michael Burn, Bronwen Whitney and Francis Mayle helped with pollen identification. Thanks also to Hannah Banks at the

Royal Botanic Gardens, Kew, for discussions concerning the identification of Fabaceae pollen

Thanks also to the herbariums at the Royal Botanic Gardens, Edinburgh and *Museo de Natural Historia,* Santa Cruz, Bolivia for permitting floral samples to be taken from herbarium reference material.

Finally, my thanks go to all those who reviewed drafts of this thesis (Francis Mayle, Toby Pennington, Michael Burn, James Ratter and Peter Furley). The comments were indispensable to the completion of this thesis.

Contents

Abstract ..... **i**

Acknowledgements ..... **iii**

Contents ..... **v**

Appendix – On CD ..... **x**

List of figures ..... **xi**

List of tables ..... **xvi**

List of equations ..... **xxi**

List of acronyms and abbreviations ..... **xxii**

Notes on the terminology and structure of the thesis ..... **xxiii**

Chapter 1. Introduction **1**

1.1. Introduction *2*

1.2. Outline of thesis *4*

1.3. Background and context of research *5*

1.3.1. Introduction to palaeoecology 5

1.3.2. Neotropical palaeoecology 6

1.3.3. Modern pollen rain studies 15

1.4. Research questions, rationale and objectives of thesis *19*

1.5. Summary of chapter *22*

Chapter 2. Study sites and ecology of neotropical savannas and seasonally dry forests **23**

2.1. Introduction to chapter *24*

2.2. Introduction to savannas and seasonally dry tropical forests *24*

2.3. Study sites *26*

2.3.1. Noel Kempff Mercado National Park 26

2.3.2. The Beni Basin 30
2.3.3. The Pantanal 33

2.4. Ecosystem ecology 34
2.4.1. The cerrado 34
2.4.2. Seasonally-inundated savannas 36
2.4.3. The Chiquitano dry forest 38

2.5. Summary of chapter 40

Chapter 3. Methodology 41

3.1. Introduction to chapter 42

3.2. Pollen sampling 42
3.2.1. Pollen traps 42
3.2.2. Lake sediment sampling 45
3.2.3. Vegetation sampling 46

3.3. Laboratory methods 47
3.3.1. Procedure for pollen processing of funnel trap samples with viscose rayon fibre 47
3.3.2. Procedure for pollen processing of sediment samples 50
3.3.3. Preparation of pollen reference material 53
3.3.4. Pollen processing of surface soil samples 54

3.4. Pollen counting 55
3.4.1. Moraceae/Urticaceae pollen differentiation 56

3.5. Summary of chapter 57

Chapter 4. Floristic differentiation of savanna and seasonally dry tropical forests in NE Bolivia 58

4.1. Introduction to chapter 59

4.2. Study sites and the ecology of neotropical savannas and seasonally dry forests 59

4.3. Methods 60
4.3.1. Vegetation sampling 60

4.3.2. Statistical methods 61

4.4. Results *66*

4.4.1. Dominant taxa 66

4.4.2. Results for savanna ordinations 66

4.4.3. Results of forest ordinations 66

4.5. Discussion *82*

4.5.1. Savanna sites 82

4.5.2. SDTF sites 84

4.6. Conclusions *86*

4.7. Summary of chapter *87*

Chapter 5. Characterisation of neotropical savannas and seasonally dry tropical forests by their modern pollen rain 88

5.1. Introduction to chapter *90*

5.2. Methodology *90*

5.3. Statistical analysis *98*

5.4. Descriptions of the vegetation of the sampling sites *100*

5.4.1. Toledo - Seasonally-inundated savanna (TO1) 100

5.4.2. Monte Verde - Seasonally-inundated SDTF (MV1) 101

5.4.3. Cerro Pelao - Upland SDTF (CP1) 101

5.4.4. Los Fierros – Upland savanna (FC1) 101

5.4.5. Los Fierros – Seasonally-inundated savanna (FT) 101

5.4.6. Description of vegetation surrounding the Beni lakes 102

5.4.7. Description of vegetation surrounding the Pantanal lakes 102

5.5. Results *109*

5.5.1. TO1 - Seasonally-inundated savanna 109

5.5.2. FC1 – Upland savanna 109

5.5.3. FT – Seasonally-inundated savanna 109

5.5.4. MV1 - Seasonally-inundated SDTF 109

5.5.5. CP1 - Upland SDTF 110

5.5.6. Beni Basin lake sediment results 110
5.5.7. SDTF lake sediment results 111
5.5.8. Pollen accumulation rates 111
5.5.9. Pollen/vegetation relationships 112
5.5.10. Moraceae/Urticaceae differentiation of NKMNP pollen traps 112
5.5.11. Comparison between pollen signals from artificial pollen traps and surface lake sediments..... 112

5.6. Discussion 133
5.6.1. Modern pollen rain from savanna ecosystems 133
5.6.2. Modern pollen rain of SDTF ecosystems..... 139
5.6.3. Pollen/vegetation relationships 144
5.6.4. Pollen accumulation rates 148
5.6.5. Inter-annual variability..... 148
5.6.6. Intra-site variability 149
5.6.7. Comparison between pollen signals from artificial pollen traps and surface lake sediments..... 151

5.7. Summary of chapter 153

Chapter 6. Differentiation of neotropical savannas and seasonally dry tropical forests by their modern pollen rain 154

6.1. Introduction to chapter 155

6.2. Statistical analysis..... 155

6.3. Results 157
6.3.1. Summary pollen diagram 157
6.3.2. Palynological differentiation of savanna ecosystems at NKMNP 157
6.3.3. Palynological differentiation of SDTF ecosystems at NKMNP 157
6.3.4. Palynological differentiation of seasonally-inundated savanna and SDTF ecosystems from surface lake sediments 158
6.3.5. Palynological differentiation of savanna and SDTF ecosystems within NKMNP 158

6.3.6 Statistical differences in pollen accumulation rates between ecosystems 159

6.4. Discussion 167

6.4.1. Differentiation of savanna ecosystems 167

6.4.2. Differentiation of SDTF ecosystems 173

6.4.3. Differentiation of savanna and SDTF ecosystems 175

6.5. Summary of chapter 181

Chapter 7. Conclusions 182

7.1. Introduction to chapter 183

7.2. Key findings of this research 183

7.3. Critical analysis of the methodology 185

7.4. Possible future research 188

References 190

Appendix – On CD

Chapter 4

Vegetation data

Ordination data tables

Chapter 5

Pollen data

Chapter 6

Ordination data tables

Pollen descriptions

List of figures

Chapter 1

Figure 1.1. Vegetation map of South America. 7

Figure 1.2. Distribution of SDTF and savannas in the Neotropics. 10

Figure 1.3. Flow diagram of the methodology of a modern pollen rain study. 15

Chapter 2

Figure 2.1. Distribution of SDTF and savannas in the Neotropics. 25

Figure 2.2. Locations and ecology of the study sites for this research. 27

Figure 2.3. Vegetation map of Noel Kempff Mercado National Park, Bolivia. 29

Figure 2.4. Aerial image of the Beni Basin, Northern Bolivia, showing the nature of the forest-savanna mosaic in the region. 30

Figure 2.5. Aerial images of the Beni Basin, Northern Bolivia, showing the nature of the forest-savanna mosaic in the region. 30

Figure 2.6. Aquatic vegetation at the margins of Laguna Azul, Beni Basin, Bolivia. 32

Figure 2.7. Extensive area of marsh vegetation between Laguna Cernandez and Laguna Belen, Beni Basin, Bolivia. 32

Figure 2.8. Open grassy savanna vegetation within the Beni Basin, Bolivia. 32

Figure 2.9. Tree-savanna within the Beni Basin, Bolivia. 32

Figure 2.10. *Campo cerrado* vegetation within NKMNP, Bolivia. 34

Figure 2.11. *Campo cerrado* vegetation within NKMNP, Bolivia. 34

Figure 2.12. *Pampa termitero* ecosystems within NKMNP, Bolivia, showing a termite mound which is covered with woody vegetation. 37

Figure 2.13. *Pampa termitero* ecosystems within NKMNP, Bolivia, showing the extensive grassy plain between the termite mounds. 37

Figure 2.14. SDTF in Eastern Bolivia. This photo was taken during the dry season and shows the deciduous nature of the forest canopy. 39

Figure 2.15. The interior of SDTF in Eastern Bolivia, showing the limited ground vegetation cover of the forest. 39

Chapter 3

Figure 3.1. Schematic of the artificial pollen trap. 43

Figure 3.2. Figure of the positioning of artificial pollen traps along a 500m baseline. 44

Chapter 4

Figure 4.1. Location of vegetation plots within NKMNP, Bolivia. 63

Figure 4.2. PCA site plot of relative cover of plant families at the savanna sites at NKMNP. 76

Figure 4.3. PCA site plot of relative cover of plant genera at the savanna sites at NKMNP. 77

Figure 4.4. PCA site plot of % of total basal area of plant families at the SDTF sites at NKMNP. 78

Figure 4.5. PCA site plot of % of total basal area of plant genera at the SDTF sites at NKMNP. 79

Chapter 5

Figure 5.1. Locations and ecology of the study sites for this research. 91

Figure 5.2. Figure showing the ecosystems surrounding the lakes sampled for their modern pollen rain from the Beni Basin. 92

Figure 5.3. Figure showing the ecosystems surrounding the two lakes sampled from the Bolivian Pantanal. 93

Figure 5.4. Figure showing the ecosystems surrounding Laguna Socorros. 94

Figure 5.5. Location of study sites within NKMNP, Bolivia. 95

Figure 5.6. Pollen percentage diagram for savanna sites within NKMNP. 113

Figure 5.7. Pollen accumulation rates for the savanna pollen traps. 115

Figure 5.8. Pollen percentage diagram for the SDTF pollen traps. 117

Figure 5.9. Pollen accumulation rates of taxa for the SDTF pollen traps. 119

Figure 5.10. Percentage pollen diagram of lake sediment data. 121

Figure 5.11. Pollen concentration diagram of lake sediment data. 123

Figure 5.12. Moraceae/Urticaceae differentiation within the pollen traps from NKMNP. 125

Figure 5.13. Cluster dendrogram of modern pollen rain from the surface lake sediments and artificial pollen traps. 126

Chapter 6

Figure 6.1. Summary pollen percentage diagram, showing all taxa with a minimum abundance of ≥3% in any one sample. 160

Figure 6.2. PCA site plot of savanna modern pollen rain samples derived from artificial pollen traps from NKMNP, Bolivia. 161

Figure 6.3. PCA site plot of SDTF modern pollen rain samples derived from artificial pollen traps from NKMNP, Bolivia. 162

Figure 6.4. PCA site plot of modern pollen rain samples of SDTF and seasonally-inundated savanna ecosystems derived from surface lake sediments from across lowland Bolivia. 163

Figure 6.5. PCA site plot of samples of modern pollen rain of SDTF ecosystems and savanna ecosystems derived from artificial pollen traps from within NKMNP, Bolivia. 164

Figure 6.6. Summary pollen diagram of Laguna La Gaiba. 179

List of tables

Chapter 1

Table 1.1. Modern pollen rain studies from savanna and SDTF ecosystems in the southern Neotropics. 17

Chapter 3

Table 3.1. Description of the five study sites for artificial pollen traps. 43

Table 3.2. Location of lakes sampled for their modern pollen rain. 46

Chapter 4

Table 4.1. Environmental attributes of the forest ecosystems within NKMNP. 64

Table 4.2. Environmental attributes of the savanna ecosystems within NKMNP. 65

Table 4.3. Percentage of stems and percentage of total basal area for family, genus and species at the AC1 site. 68

Table 4.4. Percentage of stems and percentage of total basal area for family, genus and species at the AC2 site. 68

Table 4.5. Percentage of stems and percentage of total basal area. 69

for family, genus and species at the CP1 site.

Table 4.6. Percentage of stems and percentage of total basal area for family, genus and species at the CP2 site. 69

Table 4.7. Percentage of stems and percentage of total basal area for family, genus and species at the MV1 site. 70

Table 4.8. Percentage of stems and percentage of total basal area for family, genus and species at the SR1 site. 70

Table 4.9. Relative cover and relative frequency for family, genus and species at the FO1 site. 71

Table 4.10. Relative cover and relative frequency for family, genus and species at the FO2 site 71

Table 4.11. Relative cover and relative frequency for family, genus and species at the FC1 site. 72

Table 4.12. Relative cover and relative frequency for family, genus and species at the FC2 site. 72

Table 4.13. Relative cover and relative frequency for family, genus and species at the FT site. 73

Table 4.14. Relative cover and relative frequency for family, genus and species at the H1 site. 73

Table 4.15. Relative cover and relative frequency for family, genus and species at the GC site. 74

Table 4.16. Relative cover and relative frequency for family, genus and species at the GR site. 74

Table 4.17. Relative cover and relative frequency for family, genus and species at the PP site. 75

Table 4.18. The key families on PCA axis 1 and PCA axis 2 for the savanna family level ordination. 80

Table 4.19. The key genera on PCA axis 1 and PCA axis 2 for the savanna genus level ordination. 80

Table 4.20. The key families on PCA axis 1 and PCA axis 2 for the SDTF family level ordination. 81

Table 4.21. The key genera on PCA axis 1 and PCA axis 2 for the SDTF genus level ordination. 81

Chapter 5

Table 5.1. Sampling sites of artificial pollen traps in Noel Kempff Mercado National Park. 96

Table 5.2. Sampling sites for surface lake sediment. 97

Table 5.3. Species in the MV1 plot with a percentage of total stems (with a dbh ≥10 cm) greater than 1%. 103

Table 5.4. Species in the CP1 plot with a percentage of total stems (with a dbh ≥10 cm) greater than 1%. 104

Table 5.5. Species in the FC1 plot with a percentage of total cover greater than 0.5%. 105

Table 5.6. Species in the FT plot with a percentage of total cover greater than 0.5%. 107

Table 5.7. Pollen accumulation rates of the pollen traps from NKMNP. 127

Table 5.8. P/V ratios and pollination strategy for all pollen taxa in the MV1 site with a mean ≥1%. 128

Table 5.9. P/V ratios and pollination strategy for all pollen taxa in the CP1 site with a mean ≥1%. 129

Table 5.10. P/V ratios and pollination strategy for all pollen taxa in the FC1 site with a mean ≥1%. 131

Table 5.11. P/V ratios and pollination strategy for all pollen taxa in the FT site with a mean ≥1%. 132

Chapter 6

Table 6.1. The key taxa on PCA axis 1 and PCA axis 2 for the ordination of the modern pollen rain from savanna ecosystems derived from artificial pollen traps. 165

Table 6.2. The key taxa on PCA axis 1 and PCA axis 2 for the ordination of modern pollen rain from SDTF ecosystems derived from artificial pollen traps. 165

Table 6.3. The key taxa on PCA axis 1 and PCA axis 2 for the ordination of the modern pollen rain of seasonally-inundated savannas and SDTF ecosystems derived from surface lake sediments. 166

Table 6.4. The key taxa on PCA axis 1 and PCA axis 2 for the ordination of the modern pollen rain of SDTF ecosystems and savanna ecosystems derived from artificial pollen traps from within NKMNP, Bolivia. 166

Chapter 7.

Figure 7.1. The dominant pollen taxa from artificial pollen traps from savanna and SDTF ecosystems within NKMNP. 184

List of equations

Chapter 4

Equation 4.1. Formula to calculate % of total stems. 60

Equation 4.2. Formula to calculate % of total basal area. 60

Equation 4.3. Formula to calculate relative frequency. 61

Equation 4.4. Formula to calculate relative cover. 61

Chapter 5

Equation 5.1. Formula to calculate pollen accumulation rates for artificial pollen traps. 98

Equation 5.2. Formula to calculate pollen concentration for surface lake sediments. 98

Equation 5.3. Formula to calculate pollen/vegetation ratios for savanna data. 98

Equation 5.4. Formula to calculate pollen/vegetation ratios for forest data. 99

List of acronyms and abbreviations

SDTF – Seasonally dry tropical forest

NKMNP – Noel Kempff Mercado National Park, Bolivia

PAR – Pollen accumulation rate

LGM – Last glacial maximum

^{14}C yr BP – Years before present in radiocarbon years

cal. yr BP – Years before present in calendar years

sp. – species (singular)

spp. – species (plural)

undiff. – undifferentiated

gen_indet. – indeterminable genus

fam_indet. - indeterminable family

Notes on the terminology and structure of the thesis

Many of the ecosystems studied in this thesis have a distinct terminology that is often derived from the native Portuguese or Spanish. The phrase *physiognomy* is used in this thesis to refer a specific vegetation morphology/type. The phrases *terra firme* and upland are used interchangeably to refer to a vegetation formation that grows upon soils which remain well drained all year round and are not inundated during the wet season. Vegetation formations that grow upon soils profiles that become saturated during the wet season are referred to as seasonally-inundated ecosystems.

To aid the understanding of this thesis, the definitions of some of the vegetation formations considered in this thesis will be described below.

The savannas of the Cerrado Biome of Brazil have a very variable form ranging from open grassland to almost closed woodland. There are several vernacular names given to these formations as outlined below (after Oliveria-Filho and Ratter, 2002) along with literal translations where possible.

- *Campo limpo* (clean field) is a grassland lacking trees and shrubs.
- *Campo sujo* (dirty field) is a grassland with a scattering of shrubs and small trees.
- *Campo cerrado* (closed field) has a more extensive cover of trees and shrubs.
- *Cerrado (sensu stricto*) is where the trees and shrubs have a crown cover of greater than 30% but herbaceous ground cover is still abundant.
- *Cerradão* has 50-90% crown cover of trees and shrubs with a reduced ground cover.

An issue that arises with this terminology is that “cerrado” refers to the biome as a whole and to a distinct vegetation physiognomy within this biome, hence researchers (e.g. Olivera-Filho and Ratter, 2002) have adopted the phrase “cerrado *(sensu lato)*” to refer to the full range of cerrado forms as a biome and “cerrado *(sensu stricto*)” to

refer to the distinct vegetation physiognomy within the biome. In this thesis, the phrase “cerrado” will always be referring to “cerrado *(sensu lato)”* unless defined by the addition of “*sensu stricto"* after the word "cerrado", when it will be referring to the distinct vegetation physiognomy.

There is also a wide range of different morphologies of seasonally-inundated savannas in the Neotropics. The forms with vernacular names encountered in this thesis are listed below.

- *Pampa aguada* (flooded savanna) is an open grass dominated savanna which becomes flooded during the wet season.
- *Pampa termitero* (termite savanna) consists of a flat grassy plain of graminoids and herbaceous vegetation with scattered islands of woody vegetation occurring upon raised mounds of earth, which are often occupied by a termite mound.
- *Campo rupestre* (rocky grassland) is found where soils are very thin or confined to cracks between rocks. It is normally found on the top of plateaux (Oliveira-Filho and Ratter, 2002).

Seasonally dry tropical forests (SDTF) are also studied in this thesis. They occur where rainfall is less than 1600mm/yr, with a period of at least 5-6 months receiving less than 100mm and these forest formations range from tall forests on moister sites to cactus scrub on the driest (Pennington *et al.,* 2006). In this thesis, the term SDTF will be referring to two different physiognomies of SDTF, which are semi-deciduous forest and seasonally-inundated semi-deciduous forests (after Killeen, 1998). Their physiognomy is described in detail in chapter 2.

Structure of thesis

A possible publication strategy was considered when writing this thesis. The results chapters are written in a form that aims to allow a fairly simple extraction of thesis material to potential academic papers. Therefore, there is a degree of summarising of previously introduced information (e.g. study sites, methodology) within the results chapters.

Chapter 1. Introduction

Contents

1.1. Introduction *2*

1.2. Outline of thesis *4*

1.3. Background and context of research *5*

1.3.1. Introduction to palaeoecology 5

1.3.2. Neotropical palaeoecology 6

1.3.3. Modern pollen rain studies 15

1.4. Research questions, rationale and objectives of thesis *19*

1.5. Summary of chapter *22*

1.1. Introduction

At present there is uncertainty about the type of ecosystems that existed in the Neotropics during the Quaternary. Palaeoecological research from this region has largely focused on identifying the vegetation formations that existed in Amazonia during the last glacial period and currently there are three different theories. The first is for the stability of forest cover in Amazonia during the last glacial maximum (LGM) (Colinvaux *et al.,* 2000). The second is for partial replacement of forest by more open vegetation formations such as savanna, as a response to a drier LGM climate (Haffer, 1969; Van der Hammen and Hooghiemstra, 2000). The third hypothesis is that Amazonian evergreen forest was replaced in some areas by a more open forest called seasonally dry tropical forest (SDTF) (Prado and Gibbs, 1993; Pennington *et al.,* 2000). Another time period of particular interest in the Neotropics is the Mid-Holocene. This period is a possible climatic analogue of 21st century conditions, as predicted from some global climate models (Mahli *et al.,* 2008). The response of neotropical ecosystems to the climate during the Mid-Holocene is still debated (Mayle and Power, 2008).

It is important to know the type of ecosystem that existed in the past for several reasons. Firstly, it allows the testing of biogeographic theories, for example, examining the mechanisms of speciation in Amazonia (Bush, 1995; Pennington *et al.,* 2004). It is also important for understanding and quantifying the carbon cycle, as different ecosystems have different carbon storage values (Mayle and Beerling, 2004). Therefore, knowledge of the type of ecosystems that occurred at certain time intervals can help to quantify accurately the changes in the terrestrial carbon sink during the Quaternary. Understanding the response of ecosystems to past environmental changes is also fundamentally important for any attempts to infer the response of these ecosystems to future climatic changes as caused by current global warming (IPCC, 2007). This is especially important in the Neotropics as Amazonia contains up to 25% of the world's terrestrial biodiversity (Malhi *et al.,* 2008) and

approximately 10% of the carbon that is stored in terrestrial ecosystems (Adams and Faure, 1998).

Most vegetation reconstructions from the Neotropics are derived from fossil pollen records obtained from lake sediments. The uncertainty in these reconstructions largely results from a poor understanding of the modern pollen/vegetation relationships for extant ecosystems. Additionally, neotropical pollen grains are seldom identifiable to species level and many neotropical plant taxa have species which are found in a diverse range of neotropical habitats (Marchant *et al.,* 2002). These two attributes make it difficult to infer the ecological requirements of pollen taxa and hence reconstruct the type of ecosystem that was present.

One of the most effective means of improving the interpretation of fossil pollen records is through modern pollen rain studies (Birks and Birks, 1980). This methodology involves combining a detailed survey of the vegetation of an ecosystem with an analysis of its modern pollen production. This provides pollen spectra that can be used as modern analogues to compare with fossil pollen spectra obtained from lake sediments and thus allow the type of ecosystem occurring at specific time interval to be reconstructed.

The aim of this research is to characterise different types of savanna and seasonally dry forests (SDTF) in the Neotropics by their modern pollen rain. At present, there have been few modern pollen rain studies of these ecosystems and limited attempts to differentiate different physiognomies of savanna and SDTF palynologically (Salgado-Labouriau, 1978; Ledru, 2002; Gosling *et al.,* in press). Two types of savanna will be investigated, upland savannas and seasonally-inundated savannas, and two types of SDTF, upland SDTF and seasonally-inundated SDTF. The results will then be used to test the extent to which these different ecosystems can be differentiated palynologically.

These results will be important as recognising different types of savanna and SDTF ecosystems in fossil pollen records will allow for a more accurate interpretation of

regional vegetation change. Seasonally-inundated ecosystems can change their distribution due to factors that are unrelated with climatic change, such as river migration or basin infilling, whereas the replacement of an ecosystem by upland savannas or upland SDTF, can give a clear indication of climatic changes, such as a change in precipitation.

The identification of these specific ecosystems within fossil pollen records is vitally important for testing the feasibility of the three different theories of vegetation dynamics in the Neotropics during the last glacial period and into the Holocene. For example, accurate identification of savanna ecosystems within fossil pollen records allows any evidence for replacement of forest by savanna to be inferred, whilst the recognition of SDTF signals within fossil pollen records is fundamental for testing the evidence for a possible expansion of SDTF ecosystems during this time period.

In this thesis artificial pollen traps and surface lake sediments are used to sample the modern pollen rain of savanna and SDTF ecosystems. As fossil pollen records are obtained from lake sediments, it is important to be able to compare modern pollen spectra obtained from artificial pollen traps to those from lake sediments. This allows the degree to which similar pollen spectra are obtained from both sampling environments to be tested for a given ecosystem.

1.2. Outline of thesis

The thesis commences with an introduction to the research in the context of neotropical palaeoecology. It explains the use of modern pollen rain studies in palaeoecology and outlines the research aims and rationale. The study sites and relevant vegetation types are described in chapter 2. The research methodology is described in chapter 3. Chapter 4 investigates the floristic differences between different savanna and SDTF sites under different inundation regimes. The aim is identify taxa that have a habitat preference for seasonally-inundated or well-drained (*terra firme*) areas. The modern pollen rain of the ecosystems is then described in chapter 5 and the extent to which different savanna and SDTF ecosystems can be

differentiated by their modern pollen rain is investigated in chapter 6. This is followed by a consideration of the implications for the interpretation of fossil pollen records. Chapter 7 then concludes this research.

1.3. Background and context of research

1.3.1. Introduction to palaeoecology

Palaeoecology is the study of the ecology of the past. There are numerous tools that allow us to infer past environments and these include plant macrofossils, diatoms, cladocera, molluscs, insects, vertebrate remains and pollen (Birks and Birks, 1980). This research will focus upon the use of pollen analysis; which is the most widely used method to reconstruct environments for the Quaternary time period (Lowe and Walker, 1997). The basic principles of pollen analysis (Birks and Birks, 1980) are outlined below.

1. Pollen and spores are produced by plants and these grains are identifiable to various taxonomic levels.
2. Pollen of different plants is mixed in the atmosphere resulting in a uniform pollen rain within a specific area and this pollen rain is a function of the vegetation of this area.
3. This pollen rain falls to the ground and may be preserved in environments such as lake sediments and peat bogs.
4. If a sample of peat or lake sediment of a known age is examined for its pollen spectrum, it is inferred that this pollen spectrum is a function of the vegetation that existed around the site at that time.
5. By taking numerous samples of known ages it is therefore possible to investigate the vegetation change around a site in a temporal framework.

As vegetation assemblages are a function of their climatic environment, it is therefore possible to infer palaeoclimate from fossil pollen records. For example, within the Neotropics, examining the evidence for changes in the spatial extent of evergreen forest, SDTF or savanna can be used to infer the appropriate climatic

environment at that time. This is providing that any changes in edaphic variables are also considered, as SDTF and savanna can often grow under the same climatic environment, with changes in soil fertility controlling their distribution (Ratter, 1992).

1.3.2. Neotropical palaeoecology

At present lowland humid forest covers a large area of the Neotropics, with areas of savanna and dry forest towards the periphery of the Amazon Basin (figure 1.1). However, the response of these ecosystems to the environmental changes that occurred during the Quaternary is still unresolved. A key period of study has been the LGM and most researchers have agreed on a cooling of approximately 5^{o}C during the last glacial period, however, there is still considerable uncertainty whether Amazonia was cool and dry or cool and wet at this time (Bush and Silman, 2004). Another period of interest is the Mid-Holocene as the climatic environment at this time has been inferred to be drier than at present and this period could represent a useful analogue for future conditions predicted by global climate models (Mayle and Power, 2008).

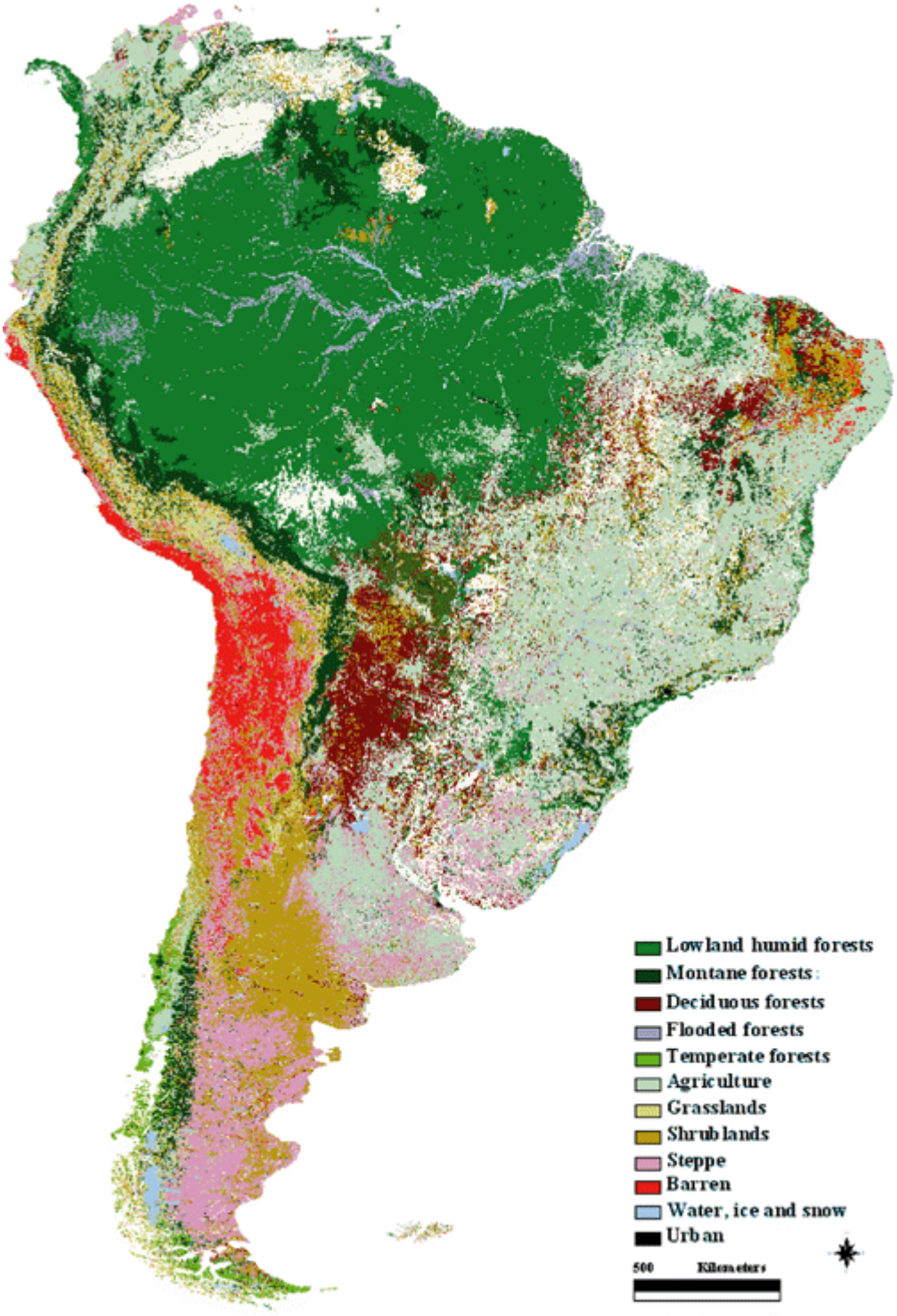

Figure 1.1. Vegetation map of South America (Eva *et al*. 2004).

One of the earliest reconstructions of glacial Amazonia was presented by Jürgen Haffer in 1969, who proposed that during glacial times the Amazon rainforest retreated into a series of small regions or "refugia" in response to lower precipitation. Haffer (1969) hypothesised that the former rainforest areas were replaced by other open, non-forest ecosystems, such as savanna, which were better adapted to the drier conditions. This theory was justified by assessing the current biogeographical distribution of Amazonian birds. This "Refugia Hypothesis" was also a possible explanation for the huge biodiversity of Amazonia which could result from the geographical separation of rainforest populations by savanna during drier periods. This would cause the isolation of rainforest populations and allow speciation events to occur through vicariance. This process could have occurred numerous times during the climatic oscillations of the Quaternary, resulting in several speciation episodes. Some fossil pollen studies from Amazonia have argued for the replacement of rainforest by savanna during the last glacial period due to a reduction in rainforest pollen and an increase in pollen types representative of savanna, such as grass and herb pollen, within sediments of glacial age (van der Hammen, 1974; Absy *et al.,* 1991 cited in van der Hammen and Hooghiemstra, 2000), agreeing with the suggestions of Haffer (1969).

More recently opposition has been presented against the Refugia Hypothesis by researchers who propose that Amazonia remained largely forested during the last glacial period, with the evidence from palynological studies of Amazonia lakes and reinterpretations of previous fossil pollen records (Colinvaux *et al.*, 1996; Colinvaux *et al.*, 2000; Bush *et al.,* 2004). The authors argue that the palynological data indicate a continuous forest cover, rather than replacement of forest by savanna, due to the very low content of herb and grass pollen found within the records. The authors inferred a cooling of temperature during the last glacial period due the invasion into the Amazonian lowlands of various Andean taxa (e.g. *Podocarpus, Humiria* and Ericaceae) that are now restricted to higher altitudes in the Andes where temperatures are cooler. Palynological analysis of sediments from the Amazon Fan in the Atlantic Ocean (Haberle and Maslin, 1999), which presumable could contain pollen types derived from across the Amazon Basin, show no evidence for the

replacement of forest by savanna. The record contained a continuous forest pollen signal with low percentages of pollen types indicative of open vegetation formations, e.g. grass and herb pollen (Haberle and Maslin, 1999). However, it has also been argued that the pollen signal within the Amazon fan may only represent riverine vegetation that grows along the margins of the Amazon river and its tributaries. This would mean that any vegetation changes in upland, *terra firme*, ecosystems would not be represented in the fossil pollen record (Burn and Mayle, 2008). It has been argued that Amazonian speciation need not invoke the Refugia Hypothesis with Bush (1994) suggesting that Pre-Quaternary events are responsible for the current major species distribution complexes.

However, these two rival reconstructions concerning the extent of forest cover in Amazonia during the last glacial period, both largely fail to identify the type of ecosystem to a resolution greater than either "forest" or "savanna". This is important as there are numerous different physiognomies of savanna and forest that occur within the Neotropics and these different ecosystems can occur under vastly different climatic and edaphic conditions.

Seasonally dry tropical forest (SDTF) presently occurs in isolated regions in the Neotropics (figure 1.2). A series of widespread species are found in these isolated regions of SDTF and it has been suggested that during the drier and cooler periods of the Pleistocene these regions may have been linked into a more continuous formation called the "Pleistocene Dry Forest Arc" (Prado and Gibbs, 1993). Pennington *et al.* (2000) suggested that SDTF may have locally replaced evergreen forest in parts of Amazonia during glacial times. This conclusion was reached by an assessment of the current distribution patterns of SDTF taxa and a reinterpretation of the pollen diagram of Colinvaux *et al.* (1996). It is inferred that climatic changes at the end of the Pleistocene would have altered the distribution of SDTF across the Neotropics. Increased precipitation in Southern Amazonia would have allowed the replacement of SDTF by evergreen forest. Further south, this would have caused a progressive leaching of the soils over the Brazilian shield, initiating a reduction in soil fertility

and causing SDTF to be replaced by the open savannas of the Cerrado Biome (Ratter *et al.,* 1988).

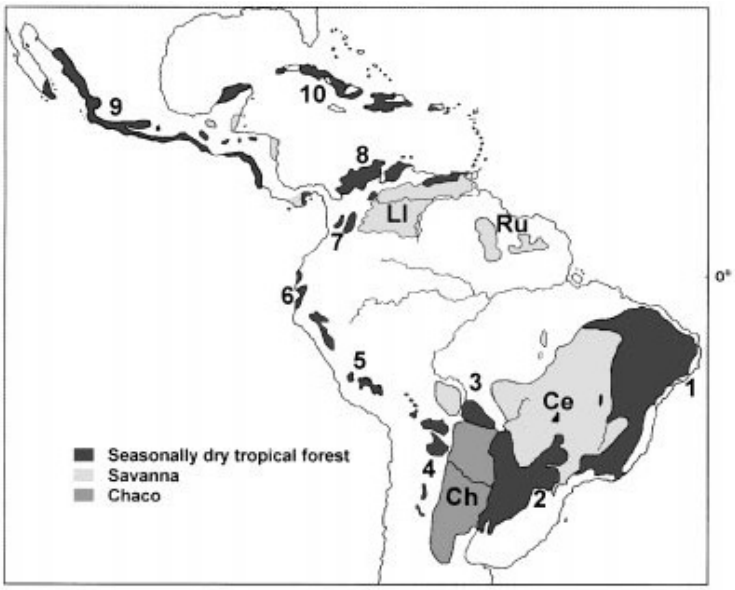

Figure 1.2. Distribution of SDTF and savannas in the Neotropics. Seasonally dry forest; 1, Caatingas. 2, Misiones Nucleus. 3, Chiquitano Region. 4, Piedmont Nucleus. 5, Bolivian and Peruvian InterAndean valleys. 6, Pacific coastal Ecuador. 7, Colombian InterAndean valleys. 8, Caribbean coast of Colombia and Venezuela. 9, Central America. 10, Antilles. Savannas: Ce, Cerrado. Ll, Llanos. Ru, Rupununi. Ch, Chaco (from Pennington *et al.,* 2000).

Palaeocological data can be used to investigate the ecosystem dynamics of SDTF areas in the past. For example, a study from within the InterAndean valleys of Colombia has shown that SDTF ecosystems have been present since the late glacial period (13450 cal. years BP) (Berrio *et al.,* 2002). Although these forests undergo a degree of floristic change the pollen signal during this period can be interpreted as representing a SDTF signal throughout the record. A second study from the area by Velez *et al.* (2005) has also shown the existence of SDTF in this area for at least the past 9000 calendar years. Research from an area currently close to the ecotone between Amazonian evergreen forest and the Chiquitano dry forest region of Bolivia (Burbridge *et al.,* 2004) has shown that SDTF existed upon upland areas around the sampling sites from 50000 cal yr BP until a few thousand years before present. These

forests were floristically different to those of the present day for most of the record, with SDTF forests floristically similar to those of today appearing during the early Holocene (9000 cal years BP). These forests then existed for most of the Holocene sequence until being replaced by evergreen forest within the last few millennia.

Evidence for the extension of SDTF during the Pleistocene can be tested using palaeoecological data, for example, palynological data from the southern margin of Amazonia (Burbridge *et al.,* 2004), shows little evidence for expansion of SDTF during the Pleistocene as does vegetation modelling of Amazonia (Mayle *et al*, 2004). It has been suggested that the current distribution of SDTF ecosystems is not due to fragmentation of a formerly more extensive "Pleistocene Dry Forest Arc" but due to long-distance dispersal of SDTF to different unconnected areas (Mayle, 2004; Mayle, 2006). However, molecular ecological data from the SDTF species, *Astronium urundueva*, has argued for the existence of a previously more extensive SDTF formation (Caetano *et al.,* 2008). More data are required to provide a definitive test of this "Pleistocene Dry Forest Arc" hypothesis.

The floristic similarity between areas of SDTF can be low (Pennington *et al.,* 2006) and the pollen signature of SDTF is currently poorly known due to the limited modern pollen research of this ecosystem. Therefore, the provision of modern pollen analogues of SDTF could help improve the recognition of this ecosystem in fossil pollen records, with relevance to the testing of the "Pleistocene Dry Forest Arc" hypothesis.

A reanalysis of the available data from Amazonia by Mayle *et al.* (2004) concluded that much of the Amazon remained forested at the last glacial maximum (LGM). The reconstruction encompasses elements from many previous studies and suggests that populations of Andean taxa increased in Amazonia, humid evergreen forests covered the central and north-western parts and SDTF taxa may have become more important in parts of the south. However there is evidence of contraction of the savanna-rainforest ecotones during the LGM in both the north (Behling and Hooghiemstra, 1999) and the south of Amazonian (Mayle *et al.,* 2000; Burbridge *et*

al., 2004), in response to cooling, drying and reduced atmospheric CO_2 concentrations.

Palaeoecological studies have also investigated vegetation change in the Cerrado Biome of Brazil (figure 1.2). This vast biome occurs to the south of the Amazon forest and covers 22% of Brazil with extensions into eastern Bolivia and NE Paraguay (Oliveira-Filho and Ratter, 2002). The Cerrado Biome has high biodiversity and plant endemism (Cavalcanti and Joly, 2002). Therefore, investigating the past dynamics of this biome through palaeoecological studies is important to understand the mechanisms of this biodiversity and to allow inferences to be made about its response to future global change.

Two sites from the centre of this biome show alternations in the extent of grassland, gallery forest and tree-savanna (cerrado) during the late Quaternary (Ferraz-Vicentini and Salgado-Labouriau 1996; Barberi *et al.,* 2000). These changes have been used to interpret the palaeoclimatic changes in this region, with a wet and cool phase being inferred for the period from 32000 ^{14}C yr BP to ~20000 ^{14}C yr BP. A dry period then following until the mid-Holocene (~5000 ^{14}C yr BP) when the vegetation began to resemble modern conditions of tree-savanna, gallery forests and palm swamps. Pollen records also exist from the southern parts of the Cerrado Biome in SE Brazil and these records have shown that during the pre-glacial and full glacial times, modern tropical semi-deciduous forest and cerrado savannas were replaced by grassland and subtropical gallery forests in response to a much cooler climate (Behling, 2002). Another site in SE Brazil shows the replacement of cerrado savannas by semi-deciduous forest during the late Holocene in response to an increase in precipitation in this area (Behling, 1995).

Palaeoecological studies from the margins (ecotones) of forest ecosystems are especially important as these areas are most sensitive to environmental changes and therefore changes in ecosystems are most likely to be observed in these areas. Data from Colombia has shown that there has been extension of forest into savanna during the Holocene (Behling and Hooghiemstra, 2000), due to a decreasing annual dry

season duration. Data from the southern margins of Amazonia also show that there has been extension of Amazonian evergreen forest into more open vegetation formations over the past 3000 years (Mayle *et al.*, 2000; Burbridge *et al.,* 2004) and this is inferred to be in response to declining seasonality reducing the length of the dry season in this region. Evidence of rainforest expansion has been inferred to be continuing to the present day due to the occurrence of relict savanna trees of the species, *Pterodon pubescens,* several kilometres into the forest from the current forest/savanna ecotone within Brazil (Ratter *et al.,* 1978).

Gallery forests are found along watercourses in the Cerrado Biome. They are important migration routes for plant and animal species and can link different floristic regions e.g. the Amazonian and Atlantic rainforests (Oliveira-Filho and Ratter, 1995). Studies across the ecotone between the gallery forest and savanna has shown evidence of variations in the relative extent of these ecosystems and palaeoecological studies have shown that gallery forests have been expanding into the savanna areas within Brazil since 3000-4000 years BP (Silva *et al.,* 2008).

The provision of modern pollen rain signatures from savanna ecosystems could help accurately reconstruct vegetation dynamics from these regions with particular implications for interpreting ecosystem change at forest-savanna ecotones.

Analysis of the available data from the Holocene has shown that there are distinct periods of climatic change (Mayle and Power, 2008). The Holocene has been relatively well studied in the Neotropics compared to the Pleistocene as the number and resolution of sediment cores from the Holocene is generally much greater and this allows detailed, high resolution records to be obtained. A distinct drying event has been inferred from several neotropical sites during the Mid-Holocene. For example, there is evidence of the replacement of forest by savanna from a site in Amazonian Brazil (Sifeddine *et al.,* 2001) and some ecotonal areas that are now covered by forest were open savanna ecosystems during this time (Mayle *et al.,* 2000; Behling and Hooghiemstra, 2000). There are also areas of forest that show

floristic and possible physiognomic changes during this period (Mayle and Power, 2008).

The significance of the Mid-Holocene in the Neotropics is that the climate was drier than it is at present (Mayle and Power, 2008). As some global climate models predict significant drying in the Amazon during the 21st century (Mahli *et al.,* 2008), the Mid-Holocene may be used as an analogue to test the resilience and sensitivity of neotropical ecosystems to a drier climate. Improving the resolution of palaeoecological interpretations is vital to enhance our appreciation of changes during this time period.

This sections shows that there is evidence of changes in the extent of evergreen forest, SDTF and savanna in the Neotropics during the Quaternary. These data are often also used to infer palaeoclimate. However, there is often uncertainty in defining the type of forest or savanna that is represented in the fossil pollen record and this has implications for these palaeoclimatic interpretations. For example, the fossil pollen record from Lake Pata in central Amazonia (Colinvaux *et al.,* 1996) was interpreted by the authors to contain taxa that were representative of continuous evergreen forest cover. However, Pennington *et al.* (2000), remarked that many of these taxa were also common in SDTF ecosystems. This distinction is important for palaeoclimate as these two ecosystems can exist under different climatic environments. Another example is the Holocene section of a fossil pollen record from NKMNP in Bolivia, which has been interpreted to represent savanna ecosystems (Mayle *et al.,* 2000). However, it is unclear whether the signal represents upland savannas or seasonally-inundated savannas. This also has importance for palaeoclimatic interpretations, as the presence of seasonally-inundated savannas upon the landscape could merely reflect an edaphic savanna that occurs due to a specific flooding regime, whereas, the presence of upland savannas would indicate that the climate was dry enough to restrict the development of forest over the landscape. The following section introduces a methodology to improve the reconstruction of neotropical ecosystems.

1.3.3. Modern pollen rain studies

The reconstruction of past ecosystems is improved through modern pollen rain studies, which are considered the most useful means of interpreting fossil pollen records (Birks and Birks, 1980). The theory of modern pollen rain studies is that if the modern pollen rain of an ecosystem is obtained, then this may be used as an analogue to compare with a fossil pollen assemblage. If the fossil and modern pollen spectra are similar then it is inferred that a similar ecosystem to the present existed during that time interval. The methodology of a modern pollen study is detailed in figure 1.3.

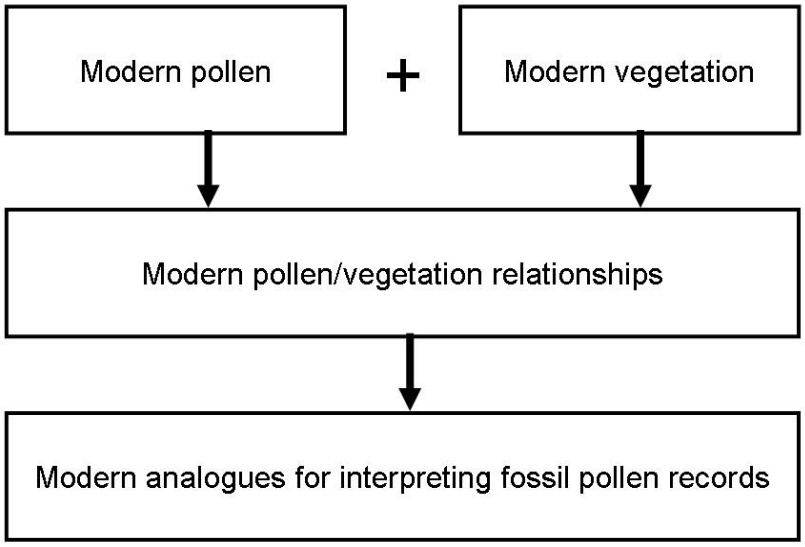

Figure 1.3. Flow diagram of the methodology of a modern pollen rain study.

Modern pollen rain studies have been successfully used to aid the interpretation of fossil pollen records. For example, Wright *et al.* (1967) conducted a detailed survey of the contemporary vegetation and pollen rain of numerous ecosystems in Iran. They collected soil samples or patches of moss and processed these to extract the pollen grains that they contained. They then visually matched these modern pollen spectra to the fossil pollen assemblages obtained from a sediment core from a lake, allowing a much more detailed interpretation of the record than was previously possible. A study from the Boreal forest of Canada (Ritchie and Yarranton, 1978)

used multivariate statistics (principal components analysis) to match modern pollen rain spectra to fossil pollen spectra of different ages and from different sites to allow a detailed analyses of vegetation change in a region. Within the Neotropics, Weng *et al.* (2006) used modern pollen rain data from an altitudinal transect of various Andean ecosystems (Weng *et al.,* 2004) to improve the reconstruction of altitudinal shifts in vegetation assemblages during the late glacial and Holocene. This detailed reconstruction then enabled a chronology of climatic change for the region to be established.

Preliminary research by Bush (1991) has shown that the major lowland neotropical vegetation types (seasonally-inundated forest*, terra firme* forest, semi-deciduous forest and savanna) are distinguishable by their modern pollen rain. However, this was very preliminary research and the paper considered few samples that were spread over South America and Central America. The palynological differences between samples could have resulted from the sites having large floristic differences due to their large geographical separation, as Neotropical ecosystems are known to be floristically heterogeneous (Ratter *et al.,* 1996). Also, savanna ecosystems were represented by just one sample. More recent modern pollen rain studies from the Neotropics have focused on altitudinal transects of different vegetation types along the flanks of the Andes (Weng *et al.,* 2004; Reese and Liu, 2005). However, there has still only been limited subsequent research into the modern pollen rain of savanna and SDTF of the southern neotropical lowlands (table 1.1), especially with regard to differentiating different physiognomies of these ecosystems. Additionally, these studies have not considered the modern pollen rain of seasonally-inundated savannas or seasonally-inundated SDTF ecosystems as this research proposes.

Reference	Ecosystem sampled	Method	Site
Salgado-Labouriau (1973, 1978)	Savanna	Pollen traps	Goias, Central Brazil
Ledru (2002)	Savanna and SDTF	Surface samples	Mato Grosso, District Federal and Sao Paulo, Brazil
Gosling *et al.* (in press)	Savanna and SDTF	Pollen traps	Noel Kempff Mercado National Park, Bolivia

Table 1.1. Modern pollen rain studies from savanna and SDTF ecosystems in the southern Neotropics.

The isolated nature of modern pollen rain studies from the Neotropics means that results from these studies have to be extrapolated over large geographical distances. This is a far from ideal situation due the heterogeneity of neotropical ecosystems, whereby an ecosystem at one location may be floristically (and hence potentially palynologically) different from a site at another locality within the same ecosystem. For example, Ratter *et al.* (1996) have noted the extremely heterogeneous nature of savanna vegetation in Brazil. To solve this dilemma there is a requirement for more research into the modern pollen rain of neotropical ecosystems.

There are two different methodologies to obtain the modern pollen rain of an ecosystem, artificial pollen traps and surface lake sediments. The purpose of a pollen trap is to capture and retain pollen grains from the surrounding environment. Various different designs of artificial pollen traps have been used in neotropical ecosystems and these range from the use of sticky slides (Salgado-Labouriau, 1978), which simply capture the airborne component of the atmosphere, to the use of funnel traps (Bush, 1992), which contain a trapping medium to capture pollen grains from the atmosphere.

Another method of obtaining the modern pollen rain of ecosystems is through surface lakes sediments. These contain pollen that enters the lake by riverine input, rain-wash and atmospheric deposition. This pollen gradually sinks and accumulates at the sediment surface.

A key advantage of artificial pollen traps is that they allow the calculation of pollen accumulation rates as the period of pollen deposition is known (usually 1 year). Pollen accumulation rates allow the number of pollen grains entering the trap per year to be calculated and they are very useful as they allow annual variation in the pollen productivity of an ecosystem to be investigated. The pollen content of a sample is most frequently presented as percentage data (Faegri and Iverson, 1989) and one problem of this is that the percentage of one taxon is dependent upon the percentage of another. Pollen accumulation rates can be used to recognise whether a decrease in the percentage abundance of a specific taxon is a genuine decrease or whether it is a "relative" decrease caused by another taxon producing more pollen, therefore reducing the percentage of the former taxon in a pollen diagram. Another advantage of pollen traps over lake sediments is that the traps can be used to obtained data from any location, whereas if surface lake sediments are used to research the modern pollen rain of an ecosystem, the samples will be limited to those geographic areas which contain lakes.

The disadvantage of artificial pollen traps is that they only capture the airborne component of the modern pollen rain and ignore the component which is transported into a sedimentary environment by stream flow. The traps are also likely to be influenced by the vegetation immediately around the trap, hence pollen from these species is likely to be over-representated within the traps. This problem can be overcome by placing several traps within the site so that an average pollen rain of an ecosystem can be obtained. Pollen traps are usually collected after one year in the field. As the composition of modern pollen rain varies on an annual basis (Fontana, 2003; Gosling, 2004), it is best to monitor the pollen rain over a period of several years, to reduce the possibility of non-representative results.

A key advantage of obtaining the modern pollen rain of an ecosystem from surface lake sediments is that they are directly comparable with fossil pollen records as they are both sampled from the same environment. The disadvantage of surface lake sediments is that they are likely to contain pollen from a mix of different vegetation types as the pollen will come from aquatic/semi-aquatic vegetation as well as the vegetation immediately surrounded the lake and pollen carried in from other more distant ecosystems by river inflow to the lake. Hence, the modern pollen rain signal from these surface lake sediments is likely to represent a mixture of different vegetation types, restricting its applicability as a modern pollen analogue for defining solely the ecosystem surrounding the lake. The duration of accumulation for surface lake sediments is difficult to define, due to factors such as bioturbation, which can result in sediment mixing. Therefore, the calculation of pollen accumulation rates from surface sediment will have much larger errors than those calculated using pollen traps.

The above paragraphs describe the relative advantages and disadvantages of artificial pollen traps and surface lake sediments as methods for obtaining the modern pollen rain of an ecosystem. In this thesis, data from artificial pollen traps is augmented by surface lake sediments from within seasonally-inundated savannas and SDTF ecosystems across lowland Bolivia so that a comparison can be made between the pollen spectra obtained from these two methods.

1.4. Research questions, rationale and objectives of thesis

The first aim of this thesis is to characterise different types of neotropical savanna (upland and seasonally-inundated savannas) and seasonally dry forests (upland and seasonally-inundated SDTF) by their modern pollen rain. The data can then be used to allow improved resolution of fossil pollen records from the Neotropics. For example, with regard to the three current hypotheses of vegetation change in the Neotropics during the LGM mentioned in section 1.3.2, this research will help to provide modern pollen analogues for different savanna ecosystems. This will aid the

recognition of these ecosystems in neotropical fossil pollen records, allowing more reliable vegetation reconstructions from a site so that the degree of replacement of evergreen forest by savanna during the LGM can be investigated.

With regard to the "Pleistocene Dry Forest Arc" hypothesis, modern pollen analogues of different SDTF formations and different savanna vegetation formations could help to recognise these ecosystems in areas postulated to be within this previously more extensive dry forest arc. This would allow vegetation reconstructions to be used to test the evidence for expansion of SDTF ecosystems across the southern Neotropics and within Amazonia.

These modern pollen rain analogues will also have implications for the reconstruction of vegetation assemblages during the Holocene. Improving the resolution of the dynamics of evergreen forest, SDTF and savanna in this period will allow the response of ecosystems to climatic changes to be studied in detail.

There has also been little attention given to characterising the type of savanna or SDTF that is inferred to exist in fossil pollen records and the second aim of this thesis is to differentiate different physiognomies of savanna and SDTF by their modern pollen rain. For example, two different savanna ecosystems that exist are seasonally-inundated savannas, which are often found within the floodplains of rivers and other areas where the water table seasonally intersects the surface (Killeen, 1998; Killeen *et al.,* 2003), and upland (*terra firme)* savannas, which are located in areas where the soil is not waterlogged during any point of the year (Eiten, 1972). It is important to attempt to differentiate savanna ecosystems in fossil pollen records as whether the savanna signal is indicative of upland or seasonally-inundated savannas has important implications for the palaeoenvironmental reconstruction from the site. The presence of upland savanna in a fossil pollen record gives a much more definitive climatic signal than a change in the extent of seasonally-inundated savannas as these can change their distribution through non-climatic influences, such as river migration and basin infilling. The replacement of upland savanna by another ecosystem, e.g. forest, is likely to result from more regional environmental changes,

for example, changes in climate and/or fire frequency. For example, there is contemporary evidence of seasonally-inundated savanna replacing forest within Noel Kempff Mercado National Park in Bolivia due to a change in the flooding regime of a river and irrespective of any regional climatic changes (Killeen *et al.,* 2003). The shifting of a river channel across its floodplain will cause some areas to suffer progressively more extensive inundation, whilst others will experience an ameliorating inundation regime allowing a transition between forest and seasonally-inundated savanna at the local scale. There is also contemporary evidence of forest expanding into the upland savannas of Brazil (Ratter, 1992), in response to an increase in precipitation in the late Holocene, therefore, in this situation the forest expansion reflects a climatic change.

This project also aims to differentiate different types of SDTF. Initial modern pollen rain studies on SDTF by Gosling *et al.* (in press), suggest that pollen of *Anadenanthera* (Fabaceae – Mimosoideae) may be used as an indicator taxon of SDTF ecosystems. However, this finding is based upon data from only one site and there is concern about the associated risks of using data from only one site as an interpretational aid for fossil pollen records. The result is also from only one type of SDTF (upland semi-deciduous forest) and there are many other different types of SDTF (Navarro and Maldonado, 2005) that have not been studied palynolgically. For example, seasonally-inundated SDTF can be found along watercourses, whilst a different type of SDTF is found on upland areas with well drained soils (Killeen, 1998).

There has been little attempt to identify different types of SDTF in the Neotropics by their modern pollen rain. Recognition of these ecosystems within fossil pollen records would allow the identification of whether a dry forest signal is indicative of inundated SDTF or upland SDTF. If the signal was inferred to represent inundated SDTF then this would only represent a local signal (e.g. vegetation immediately surrounding the lake or watercourses that flow into the lake). However, if the pollen spectra is representative of upland SDTF, this would be a more regional signal, as

this ecosystem would occur away from the immediate surroundings of the site (e.g. vegetation growing on the interfluves).

To make any specific palaeoclimatic inferences from a site it is important to be able to recognise any regional changes in vegetation, as purely local changes can be affected by factors unrelated to climate such as river migration. This means that there is a necessity for more studies into the modern pollen rain of SDTF to allow more effective identification of these ecosystems by their modern pollen rain.

1.5. Summary of chapter

This chapter introduces this research project and outlines its aim to characterise and differentiate neotropical savanna and seasonally dry forest ecosystems by their modern pollen rain. It introduces the research in terms of improving our understanding of neotropical palaeoecology and describes how modern pollen rain studies are an important method of improving the interpretation of fossil pollen records, hence, improving palaeoecological interpretations from the region. The following chapter describes the study sites and the relevant types of savanna and SDTF.

Chapter 2. Study sites and ecology of neotropical savannas and seasonally dry forests

Contents

2.1. Introduction to chapter *24*

2.2. Introduction to savannas and seasonally dry tropical forests *24*

2.3. Study sites *26*

2.3.1. Noel Kempff Mercado National Park 26

2.3.2. The Beni Basin 30

2.3.3. The Pantanal 33

2.4. Ecosystem ecology *34*

2.4.1. The cerrado 34

2.4.2. Seasonally-inundated savannas 36

2.4.3. The Chiquitano dry forest 38

2.5. Summary of chapter *40*

2.1. Introduction to chapter

This chapter introduces the ecosystems to be investigated within this research. It describes the morphology and distribution of savannas and seasonally dry tropical forests (SDTF) within the Neotropics. The study sites chosen for this research are then described, along with a justification of why they were selected. This is followed by a detailed description of the different physiognomies of the specific savanna and SDTF ecosystems that are to be sampled for the modern pollen rain studies.

2.2. Introduction to savannas and seasonally dry tropical forests

Seasonally dry tropical forests (SDTF) occur in regions which have a distinct dry season and are tree-dominated ecosystems (Mooney *et al.,* 1995), whereas savannas are usually dominated by a xeromorphic grass layer (Pennington *et al.,* 2006). Both savannas and SDTF can be found under a similar climate, with variations in soil fertility and water availability often being the most important environmental variables (Ratter, 1992). There are numerous physiognomies of savanna and dry forest within the Neotropics. At a coarse resolution, these can be divided into those which suffer seasonal flooding during the wet season (seasonally-inundated ecosystems) and those with a soil profile that remains well drained throughout the year (*terra firme* ecosystems).

Neotropical savanna ecosystems have been differentiated using climatological criteria by Sarmiento (1984): (i) semi-seasonal savannas occur where there is a prolonged wet season, without an extended period of water deficit; (ii) seasonal savannas occur where there is a dry season alternating with a wet season but without waterlogging of the soil profile at any time during the year; (iii) hyperseasonal savannas occur under a seasonal climate with a dry season alternating with a wet season, with waterlogging of the soil during the wet season and a water deficit during the dry season; and (iv) marshy savannas occur where the soil profile remains saturated during the year due to a water excess.

The largest extent of savannas within the Neotropics is the cerrado (figure 2.1), which is found in Central Brazil with extensions into Eastern Bolivia and Paraguay. Other notable areas of savanna are the Llanos de Moxos savanna of Northern Bolivia, the Llanos of Colombia and Venezuela and the Rupununi savannas of Northern Brazil and Western Guayana.

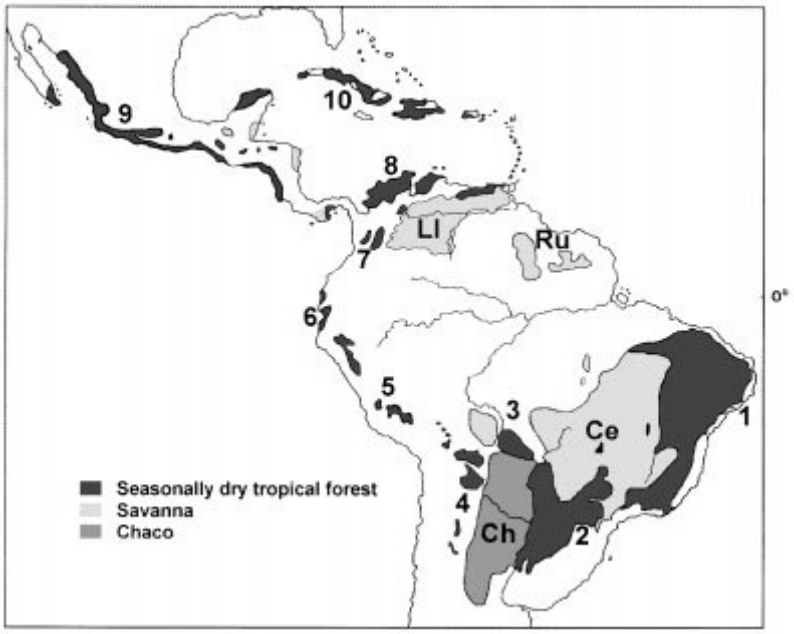

Figure 2.1. Distribution of SDTF and savannas in the Neotropics. Seasonally dry forest; 1, Caatingas. 2, Misiones Nucleus. 3, Chiquitano Region. 4, Piedmont Nucleus. 5, Bolivian and Peruvian InterAndean valleys. 6, Pacific coastal Ecuador. 7, Colombian InterAndean valleys. 8, Caribbean coast of Colombia and Venezuela. 9, Central America. 10, Antilles. Savannas: Ce, Cerrado. Ll, Llanos. Ru, Rupununi. Ch, Chaco (from Pennington *et al.,* 2000).

The extent of SDTF in the Neotropics is outlined in figure 2.1. SDTF currently has a disjunct distribution in South America, with the main areas of the vegetation being the Caatinga formation in NE Brazil, the Misiones nucleus in SW Brazil and NW Argentina, and the Chiquitano dry forest complex in Eastern Bolivia. There are patches of SDTF in the inter-Andean valleys of Peru, Bolivia and Ecuador, along with a region on the coast of Venezuela and Colombia.

2.3. Study sites

The study sites used in this research are from three different geographical regions of Bolivia and their locations are shown in figure 2.2. The map also shows the ecoregions (after Olson *et al.,* 2001) in which the study sites occur.

2.3.1. Noel Kempff Mercado National Park

NKMNP is at an ecotone between Amazonian rainforest to the north and the dry forest and savanna of the cerrado to the east and south (see figure 2.3). The annual precipitation is between 1,400mm and 1,500mm and the mean annual temperature is between 25°C and 26°C (Killeen, 1998). There is a distinct dry season from June to September, when the mean monthly precipitation is less than 30 mm (Killeen *et al.,* 2003). The limits of the park are delimited by two black-water rivers, Rio Iténez and Rio Paraguá, which originate on the Precambrian Brazilian shield and have very low sediment loads. The eastern half of the Park is dominated by a large sandstone plateau (Serranía de Huanchaca), which reaches an altitude of 900m. Most of the plateau is covered by savannas with patches of evergreen forest. The western part of the park is covered by Tertiary sediment deposits, with an altitude of 200-300m. Here, the vegetation is mostly a mosaic of inundated and *terra firme* evergreen forest, with areas of seasonally flooded savannas found along the alluvial plains of the rivers (Killeen & Schulenberg, 1998). Towards the southern margins of the park, the forests become increasingly deciduous in nature.

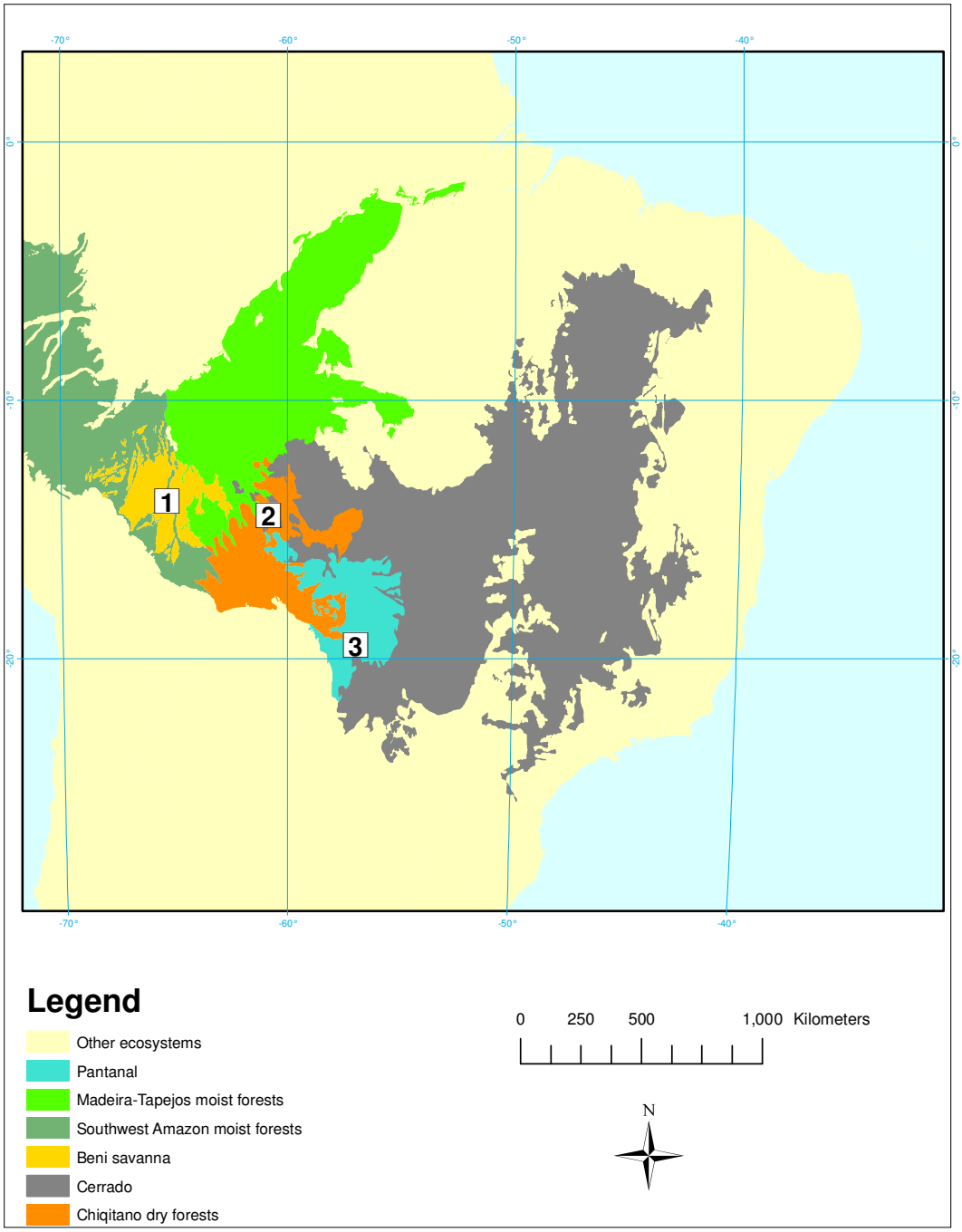

Figure 2.2. Locations and ecology of the study sites for this research. 1. The Beni Basin. 2. Noel Kempff Mercado National Park. 3. The Pantanal. Ecoregions from from Olson *et al.* (2001). Base data from http://geodata.grid.unep.ch.

NKMNP has several attributes as a site for studying the modern pollen rain of savanna and seasonally dry tropical forest ecosystems. Firstly, the park is relatively undisturbed by anthropogenic activity (Killeen and Schulenberg, 1998) so any ecosystems studied are likely to be relatively close to a natural state. This is important since the modern sites should be as undisturbed by humans as possible to allow comparisons to vegetation assemblages from the Holocene and Pleistocene which are likely to have existed in a relatively undisturbed state. Secondly, the park is located at an ecotonal region between Amazonian forest to the north, and the savanna and dry forest habitats of the Cerrado Biome to the south and east. This has the advantage that several different ecosystems are available for study within a relatively small geographical area, which is particularly useful for research in South America, where the limited infrastructure affects the accessibility of many sites. Thirdly, botanical inventories of several vegetation assemblages within the park have been collected (T. Killeen, unpublished data). If the modern pollen rain is sampled from within these vegetation plots then the contemporary relationships between vegetation and pollen production can be investigated. Fourthly, previous palaeoecological studies are available from NKMNP (Mayle *et al.,* 2000; Burbridge *et al.,* 2004). Therefore, the modern pollen rain data will be available to improve the palaeoecological interpretations from the park. Finally, the proposed study is part of a collaborative effort to define the modern pollen rain of various vegetation assemblages within NKMNP, complimenting previous research (Gosling, 2004; Burn, 2008).

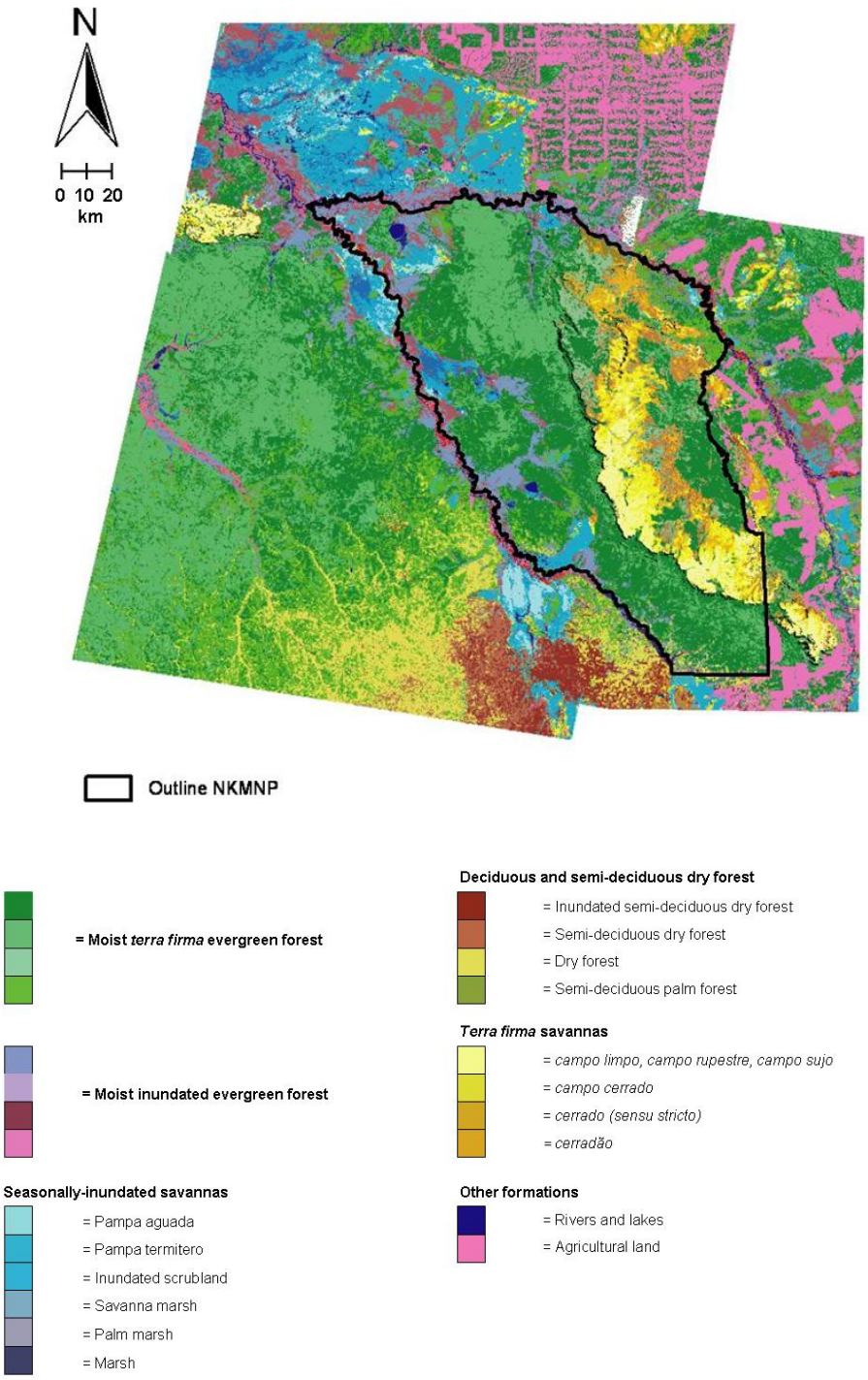

Figure 2.3. Vegetation map of Noel Kempff Mercado National Park, Bolivia (modified from Killeen and Schulenberg, 1998).

2.3.2. The Beni Basin

The Beni Basin is vegetated by a forest/savanna mosaic (figures 2.4 and 2.5). The region experiences a pronounced dry season of 4-5 months during the Austral Winter, with the wet season occurring during the Austral Summer. The district capital, Trinidad, has an annual mean precipitation of 1912 mm per annum and a mean annual temperature of 25.6^{o}C (Navarro and Maldonado, 2005). The intense rainfall of the wet season together with the extremely flat nature of the landscape results in widespread flooding of the area during this time. Many rivers of the region flood their banks and many depressions become filled by rainwater.

Numerous lakes characterise the region. Along the main watercourses these are predominantly of an ox-bow type formed by meander migration, however, away from the main watercourses, the lakes tend to have a distinct orientation from the north-east to the south-west and have a distinct rectangular shape. These orientated lakes are generally shallow with an average depth of 1m to 1.5m (Hanagarth, 1993). The origin of these lakes is still largely unresolved with some authors suggesting a tectonic origin along structural linaments in the underlying bedrock (Hanagarth, 1993), whilst others have suggested they are possibly deflation basins created during drier periods of the Quaternary, such as the last glacial maximum (Clapperton, 1993).

Figure 2.4 and 2.5. Aerial images of the Beni Basin, Northern Bolivia, showing the nature of the forest-savanna mosaic in the region.

The main rivers (Río Beni and Río Mamoré) of the region are flanked by areas of gallery forest that have been placed floristically in the Southwest Amazon moist forest ecoregion (Olson *et al.,* 2001). The areas between these rivers are characterised by open savanna formations, with scattered areas of remnant gallery forests and forest islands. The vegetation structure appears to be controlled by topographic variation and the subsequent impact that this has upon the duration/depth of inundation during the wet season. The vegetation formations (figures 2.6, 2.7, 2.8, 2.9) can be described by the inundation regime that they experience. For example Navarro and Maldonado (2005) divide the vegetation into the following units: (i) non-flooded upland vegetation (*alturas*), these areas usually avoid inundation during the wet season and are covered by either semi-deciduous forests or tree-savanna (*cerradão*); (ii) scarcely flooded vegetation (*semi-alturas*), these vegetation formations are inundated by floodwaters for 1-3 months of the year with the depth of inundation usually less than 0.8m. Areas of evergreen forest can be found along the main watercourses with savanna and forest islands found away from the rivers; (iii) seasonally flooded vegetation (*bajíos de aguas estacionales*) are inundated for several months of the year, the vegetation formations include savannas and riverine forests; and (iv) permanently flooded vegetation (*bajíos de aguas permanentes*). Around the lakes there is a fringe of aquatic vegetation, the main species being *Eichhornia* spp. *(*Pontederiaceae*), Panicum elephantipes* (Poaceae), *Marsilea crotophora (*Marsileaceae*), Polygonum densiflora* (Polygonaceae*), Thalia geniculata (*Marantaceae) and *Cyperus giganteus* (Cyperaceae) (Sanjines and Beck, 2004). Areas of floating vegetation are also present in these areas.

Figure 2.6. Aquatic vegetation at the margins of Laguna Azul, Beni Basin, Bolivia.

Figure 2.7. Extensive area of marsh vegetation between Laguna Cernandez and Laguna Belen, Beni Basin, Bolivia.

Figure 2.8. Open grassy savanna vegetation within the Beni Basin, Bolivia.

Figure 2.9. Tree-savanna within the Beni Basin, Bolivia.

The Beni has a long history of human activity, with the earliest evidence dating back about 3000 years BP (Mann, 2008). Current land use throughout the region is predominantly cattle grazing which was first introduced to the region in 1682, however, the human population density of the region is very low with a population density of just 1.3 persons per km^2 (Hanagarth, 1993). Some of these forest islands mentioned above have been suggested to be growing up on mounds constructed by humans (Denevan, 1970), however, others appear to show no evidence for an anthropogenic origin (Langstroth, 1997), with these forest islands inferred to be growing upon palaeo-levees that have been fragmented by fluvial erosion.

The Beni Basin is characterised by numerous accessible lakes within the seasonally-inundated savannas. These provide ideal sites to allow the modern pollen rain of these ecosystems to be investigated through the analysis of surface lake sediments which will contain the pollen rain of the surrounding vegetation.

2.3.3. The Pantanal

The Pantanal covers about 135000 km^2 of West-Central Brasil with extensions into Eastern Bolivia and Paraguay (Assine and Soares, 2004). The landscape is extremely flat and extensive inundation of the region occurs during the wet season, which has duration of approximately five months. The vegetation of the Pantanal consists of a mosaic of different ecosystems with the degree of inundation being the major controlling factor. For example, marshes are found in areas of permanent standing water, seasonal grassland and scrub cover the seasonally inundated areas, gallery forests can be found along the river banks and semi-deciduous forest or savanna (cerrado) occur upon the non-flooded areas (Pinder and Rosso, 1998; Ratter *et al.,* 1988; Prance and Schaller, 1982). The vegetation composition of the Pantanal is inferred to represent a mix of different phytogeograhic regions, for example, gallery forest in the region is considered to have a strong Amazonian element, whilst the savanna areas are floristically very similar to the extensive cerrado savannas found in Brazil (e.g. *Caryocar brasiliense* and *Curatella americana*), whilst the semi-deciduous forests have affinities to other dry forest areas of the Neotropics (Prance and Schaller, 1982)

The World Wildlife Fund states that the majority of the Pantanal is in a relatively undisturbed state (Male, 2001), the main economic activity within the region being cattle ranching which has caused some ecosystem modification, for example, increasing the abundance of unpalatable species in grazed areas (Prance and Schaller, 1982).

2.4. Ecosystem ecology

2.4.1. The cerrado

The Cerrado Biome covers over 2 million square kilometres (Eiten, 1972) and consists of several different assemblages of savanna type vegetation on upland regions. There are two strata to the vegetation of the cerrado, a stratum of trees and shrubs and a ground stratum of herbaceous vegetation (Furley, 1999). Soils of the cerrado are typically acid with low cation exchange capacity and high levels of aluminium saturation (Furley & Ratter, 1988). There is a wide range of vegetation physiognomies within the Cerrado Biome, these range from dry grassland without trees or shrubs at one end of the spectrum, to almost closed woodland, with crown cover of 50%-90% at the other extreme, (Oliveira-Filho & Ratter, 2002). These different morphologies are given different vernacular names (after Oliveira-Filho and Ratter, 2002): (i) *campo limpo* (clean field) is a grassland lacking trees and shrubs; (ii) *campo sujo* (dirty field) is a grassland with a scattering of shrubs and small trees; (iii) *campo cerrado* (closed field) has a more extensive cover of trees and shrubs (figures 2.10 and 2.11); (iv) *cerrado (sensu stricto)* is where the trees and shrubs have a crown cover of greater than 30% but herbaceous ground cover is still abundant; and (v) *cerradão* has 50-90% crown cover of trees and shrubs with a reduced ground cover.

Figure 2.10. *Campo cerrado* vegetation within NKMNP, Bolivia.

Figure 2.11. *Campo cerrado* vegetation within NKMNP, Bolivia.

All the cerrado physiognomies occur within NKMNP, with the main area being on the Huanchaca Plateau (figure 2.3), with small outcrops within the lowland plains in

the western area of the park. Within the Beni Basin and the Patanal, cerrado physiognomies can be found upon land that is above the seasonal inundation level. In the Beni Basin these areas are locally called *alturas* and in the Pantanal they have the local name of *cordilheiras* or *capões* (Ratter *et al.,* 1988; Navarro and Maldonado, 2005).

Most cerrado species are intolerant of water logging (Eiten, 1972) and this is the reason that cerrado is an upland formation with other vegetation units (gallery forest or seasonally-inundated grassland) being prevalent in the more moist environments. A topographic sequence is often observed along slopes in the Cerrado Biome, with cerrado vegetation present along the upland areas of the gradient where the soil is well drained. As the water table approaches the ground surface down slope there is a change in the vegetation to an open grassy, seasonally-inundated savanna. At the base of the slope, close to the watercourse, gallery forest is often present due to the presence of moist soils (Furley & Ratter, 1988). Fire is a key factor within the Cerrado Biome and there is palaeoecological evidence of fire within the Cerrado Biome dating back to 27,000aBP (Vicentini, 1993, cited in Hoffman and Moreira, 2002). Cerrado vegetation often shows numerous adaptations to withstand fire, such as thick, corky, fire resistant-bark, sclerophyllous leaves and xylopodia (Furley & Ratter, 1988).

There have been numerous attempts to explain the factors which control the existence of these different savanna morphologies and an increasing woody component of the cerrado savannas has been correlated with a decreasing fire frequency and an increasing surface soil fertility (Furley, 1999). Some researchers have suggested that the climax vegetation of the Cerrado Biome is *cerradão*, with the other physiognomies being intermediate successional phases after a fire (Henriques and Hay, 2002) and that the protection of cerrado areas from fire results in a shift from more open vegetation formations towards closed forest (Durigan & Ratter, 2006), whilst frequent burning favours the development of herbaceous vegetation.

Alpha diversity is high with sometimes over 100 species of woody vegetation growing together within a cerrado community (Ratter *et al.,* 2003). The dominant woody taxa in terms of species number are Leguminosae (153), Malpighiaceae (46), Myrtaceae (43), Melastomataceae (32) and Rubiaceae (30) (after Heringer, 1977 cited in Oliviera-Filho and Ratter, 2002). There has only been limited investigation of the ground flora of the cerrado, however, a study by Munhoz & Felfifi (2005) investigated the floristics of the ground layers of a *campo limpo úmido* (moist grassland) in Central Brasil. They found the richest families to be Cyperaceae, Poaceae, Xyridaceae, Eriocaulaceae, Asteraceae, Orchidaceae and Melastomataceae. A review by Filgueiras (2002) stated that the dominant families in the non-arboreal category are the Leguminosae, Compostitae, Poaceae and Orchidaceae.

2.4.2. Seasonally-inundated savannas

These savannas occur in areas where the soil profile is waterlogged during the wet season but dries out during the dry season. Due to these contrasting stresses of seasonal water-logging, followed by seasonal water-deficit, most of these areas do not have a well developed stratum of woody plants (Killeen, 1998) and herbaceous cover dominates these areas.

Within NKMNP, a number of different physiognomies of seasonally-inundated savanna exist and one type under study in this thesis is locally called *pampa termitero*. Within NKMNP, this ecosystem (figures 2.12 and 2.13) consists of a flat grassy plain of graminoids and herbaceous vegetation with scattered islands of woody vegetation occurring upon raised mounds of earth, which are often occupied by a termite mound. These mounds are typically about 1m above the surrounding plain and have a diameter of 1m to 4m. During the wet season the grassy plain is inundated by flood water, whilst the raised mounds remain above the water level, allowing them to be colonised by woody vegetation that would otherwise be intolerant of the inundation regime present in this ecosystem. Within the Beni Basin, numerous physiognomies of seasonally-inundated savanna occur in the *bajios* and

semi-alturas. Within the Pantanal vast extensions of seasonally-inundated grasslands and seasonal swamps occur (Ratter *et al.,* 1988).

The *pampa termitero* ecosystem in Bolivia is similar to the *campo de murundus* ecosystems described in the Brazilian literature which are open grasslands with scattered raised earthmounds bearing cerrado shrubs and trees (e.g. Oliveira-Filho and Ratter, 2002) The origin of these mounds has been debated in the literature with termite activity (Oliveira-Filho, 1992a) or differential erosion of the substrate by floodwaters (Diniz de Araujo Neto *et al.,* 1986; Furley, 1986) being attributed to their formation. More recent research has attributed their origin to a combination of both factors (Ponce & Da Cunha, 1993).

Figure 2.12. *Pampa termitero* ecosystems within NKMNP showing a termite mound which is covered with woody vegetation.

Figure 2.13. *Pampa termitero* ecosystems within NKMNP showing the extensive grassy plain between the termite mounds.

Oliveira-Filho (1992b) found that the number of species upon an earth mound was correlated with the surface area of the mound and that there was a distribution of species from the margins of the mound to the centre, correlated with their toleration of water-logging. The more tolerant species will be found towards the margin of the mound, with the least tolerant species towards the centre. The woody vegetation that colonises these mounds has been inferred by some authors to be a subset of the cerrado flora that is most tolerant of inundation (Oliveira-Filho, 1992b). However this viewpoint is contradicted by research within NKMNP by Killeen (1998), who asserts that although some colonists are typical cerrado species, others are not common cerrado taxa within the park.

Campo rupestre (rocky grassland) is a type of grassland that occurs on plateaux and mountain ridges within the Cerrado Biome. The very thin soils are confined to cracks between the exposed bedrock and hence are rapidly waterlogged during the wet season, yet rapidly dry out during the dry season (Oliveira-Filho & Ratter, 2002). The consequence of the thin soil is that herbaceous communities dominate as the soil depth is not great enough to permit a wide cover of woody plants. A review of this ecosystem within Brazil by Filgueiras (2002), found the dominant families in this formation to be Compositae (169 spp.), Leguminosae (107 spp.), Melastomatacae (90 spp.), Eriocaulacae (84 spp.) and Orchidaceae (80 spp.).

Inundated grassland (*pampa aguada)* is another type of seasonally-inundated savanna that occurs within NKMNP. This ecosystem is discernible from *pampa termitero* due to the lack of termite mounds and the associated woody vegetation, hence herbaceous vegetation tends to dominate. The lack of termite mounds may be attributed to the greater inundation depth (up to 2 m) that this ecosystem experiences relative to the *pampa termitero.*

The boundary between these seasonally flooded savannas and adjacent forests is often very well defined and studies by Furley & Ratter (1990), deduced the controlling factor on this boundary as the limit of seasonal flooding, with the forest occuring on well drained soils and the savanna where seasonal waterlogging occurs.

Within NKMNP (figure 2.3), these ecosystems are mostly found upon the Tertiary sediments in the western areas of the park and along the watercourses of the Rio Iténez and Rio Paraguá. *Campo rupestre* is found along the exposed margins of the Huanchaca plateau.

2.4.3. The Chiquitano dry forest

The main extent of SDTF in Bolivia is the Chiquitano dry forest complex (figures 2.14 and 2.15). SDTF and cerrado can often form a mosaic pattern and the main control upon the distribution of SDTF and cerrado appears to relate to soil fertility,

with a change from mesotrophic or eutrophic soils to dystrophic soils controlling the transition from SDTF to cerrado (Ratter, 1992).

Figure 2.14. SDTF in Eastern Bolivia. This photo was taken during the dry season and shows the deciduous nature of the forest canopy.

Figure 2.15. The interior of SDTF in Eastern Bolivia, showing the limited ground vegetation cover of the forest.

Within the vicinities of NKMNP there are four different types of SDTF. These forests are a northern extension of the Chiquitano dry forest region (Killeen, 1998), which is believed to be the largest remaining area of SDTF within the Neotropics (Parker, 1993). Floristically, this forest grades into the Amazonian forest to the north and the Gran Chaco to the south (Killeen *et al.,* 1998) and the degree of deciduousness increasing from north to south with the more southern areas being completely deciduous (Killeen *et al.,* 2006). SDTF is mostly found just to the south of NKMNP and three different morphologies of SDTF are considered within this thesis. One is semi-deciduous forest, which grows on well drained soils in NKMNP. It has a canopy height of 15-20m, with occasional emergent trees to 25m and a limited ground vegetation cover. Within the vicinities of NKMNP, the dominant

species are *Anadenanthera colubrina, Casearia gossypiosperma, Amburana cearensis, Combretum leprosum, Tabebuia insignis, Tabebuia serratifolia, Eriotheca roseorum, Poeppigia procera,* and *Aspidosperma cylindrocarpon* (Killeen, 1998). The Chiquitano dry forest has been found to have floristics similarities to two other SDTF areas outlined in figure 2.1, namely, the Misiones Nucleus of eastern Paraguay and north-eastern Argentina, and the Caatinga of NE Brazil (Killeen *et al.,* 1998). Within the Beni Basin and the Pantanal, outcrops of the Chiquitano dry forest can be found upon the upland areas that are not inundated during the wet season (Ratter *et al.,* 1988; Navarro and Maldonado, 2005).

Another type of SDTF under study is a tall seasonally-inundated semi-deciduous forest, which grows on poorly drained soil. In NE Bolivia, this ecosystem can form a mixed dendritic pattern with a type of forest called semi-deciduous palm forest which is dominated by *Attalea speciosa* (Killeen, 1998). The semi-deciduous palm forest tends to occur on the higher areas with the seasonally-inundated SDTF occurring upon areas of poorly drained soils.

2.5. Summary of chapter

This chapter outlines the ecology of the different types of savanna (upland savanna and seasonally-inundated savanna) and seasonally dry tropical forest (upland and seasonally-inundated SDTF within the Chiquitano dry forest) ecosystems studied in this research. It introduces the study sites and explains why they were chosen as locations for a modern pollen rain study. The following chapter explains the methodologies used to sample the vegetation and modern pollen rain of these ecosystems.

Chapter 3. Methodology

Contents

3.1. Introduction to chapter *42*

3.2. Pollen sampling *42*

3.2.1. Pollen traps 42

3.2.2. Lake sediment sampling 45

3.2.3. Vegetation sampling 46

3.3. Laboratory methods *47*

3.3.1. Procedure for pollen processing of funnel trap samples with viscose rayon fibre 47

3.3.2. Procedure for pollen processing of sediment samples 50

3.3.3. Preparation of pollen reference material 53

3.3.4. Pollen processing of surface soil samples 54

3.4. Pollen counting *55*

3.4.1. Moraceae/Urticaceae pollen differentiation 56

3.5. Summary of chapter *57*

3.1. Introduction to chapter

This chapter describes the methodologies that were used to investigate the modern pollen rain of different savanna and seasonally dry forest ecosystems. Both artificial pollen traps and surface lake sediments were used to capture the modern pollen rain of the ecosystems studied and these are described along with the strategy for sampling the vegetation of the study sites. The laboratory protocols for extracting the pollen grains from these two trapping media are detailed, along with the protocol to prepare modern pollen reference collection material from herbarium samples that are used to aid the identification of different pollen grains. The pollen counting and sampling strategy methodologies are also described.

3.2. Pollen sampling

3.2.1. Pollen traps

Sampling of the artificial pollen traps was performed by Francis Mayle and William Gosling between 1999 and 2001. For this research a modification of the artificial pollen trap designed by Bush (1992) was adopted for several reasons (after Gosling, 2004); (1) portability; (2) cheapness; (3) simplicity, as the traps could be constructed from materials readily available in the region; (4) it can withstand the high rainfall typical of the Neotropics. Full details of the pollen trapping methodology are available in Gosling *et al.* (2003) and are summarised here. The trap consists of a plastic funnel with a diameter of 70 mm, which contains a Whatman glass fibre filter paper and viscose rayon fibre (figure 3.1). The trap is then surrounded by a coarse plastic mesh to hold the contents in place.

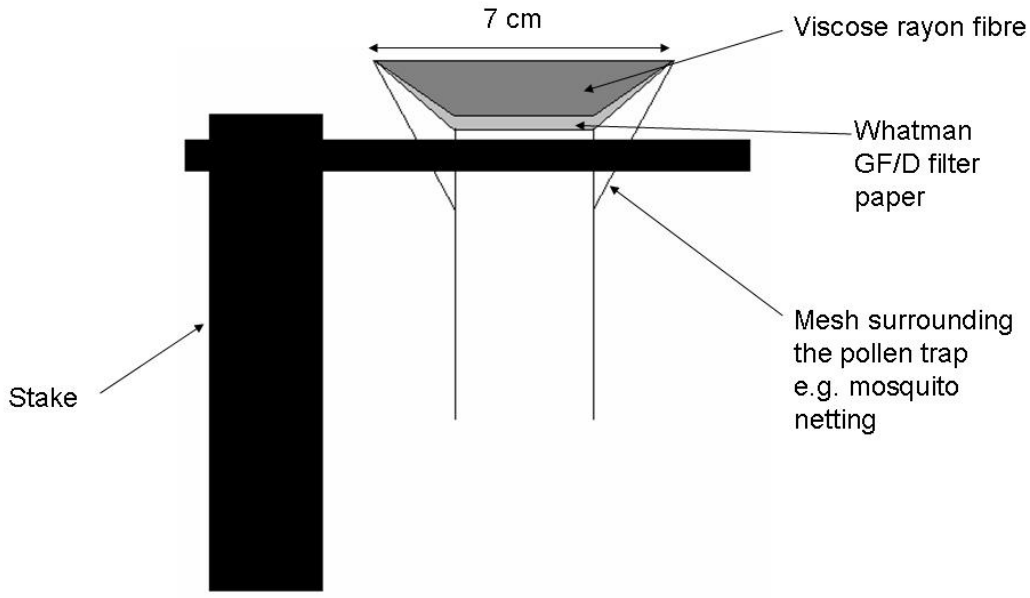

Figure 3.1. Schematic of the artificial pollen trap (modified from Gosling *et al.,* 2003).

The constructed pollen traps were then mounted to a wooded stake and placed within five different ecosystems under investigation (table 3.1).

Plot	**Latitude (S)**	**Longitude (W)**	**Site name**	**Ecosystem**	**Inundation regime**	**Altitude (m)**
FC1	14°36'25"	60°51'23"	Los Fierros	Cerrado savanna	None	200
FT	14°36'53"	60°51'59"	Los Fierros	Termite savanna	Seasonal	200
CP1	14°32'28"	61°29'53"	Cerro Pelao	Deciduous forest	None	400
TO1	14°43'41"	61°08'16"	Toledo	Termite savanna	Seasonal	200
MV1	14°56'27"	61°07'59"	Monte Verde	Seasonally inundated semi-deciduous forest	Seasonal	230

Table 3.1. Description of the five study sites.

The pollen traps at each study site were placed within 500 m × 20 m permanent vegetation plots for which detailed botanical inventories are available through the SALVIAS database (SALVIAS, 2002). Ten traps were placed 50 m apart along a 500 m baseline within the ecosystem (figure 3.2) and this baseline was aligned with the long axis of the vegetation plot. The vegetation plots were relocated each year with the aid of local field assistants and GPS.

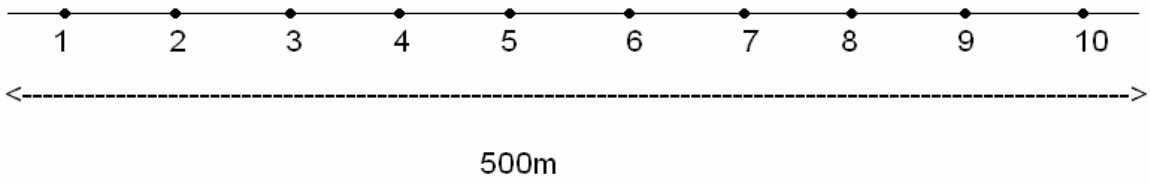

Figure 3.2. Figure of the positioning of artificial pollen traps along a 500 m baseline.

Within *terra firme* ecosystems the traps were placed 50 cm above the ground surface and for seasonally-inundated ecosystems the traps were placed 50 cm above the estimated inundation level. Other pollen traps are often located at ground level (Bush, 1992; Hicks *et al.,* 2001), however, for this study it was decided to locate the pollen traps above ground level to prevent the trap being covered by leaves/dead vegetation and minimise fire damage.

The traps were collected after a year in the field and then placed within sealed plastic bags and stored at 4^{o}C until processed. The sampling was conducted over a 3 year period (1999-2001), so that the inter-annual variability in the modern pollen rain could be observed. Pollen rain has been observed to be highly variable on an annual basis (Autio and Hicks, 2004; Gosling *et al.,* 2005), therefore, if just one year of sampling was performed, there is a risk that that year's pollen signal may not be representative of the ecosystem over a longer time period. Fossil pollen samples obtained from lake sediments are likely to be a composite of many years of pollen accumulation, therefore it is important to sample several years of the modern pollen rain of an ecosystem.

3.2.2. Lake sediment sampling

The surface lake sediments of several lakes within savanna and seasonally dry tropical forest were sampled for this thesis (see table 3.2). A perspex tube and piston were used to collect the surface lake sediment. The surface core was extruded in the field and the top 0-1 cm section was sectioned into a sample vial and then stored at 4^{o}C in a dark environment until processed. The samples from 2001 and 2002 were collected by Francis Mayle (University of Edinburgh), whilst the samples from 2006 were collected by the author.

Lake	Latitude (S)	Longitude (W)	Ecosystem	Year sampled	Surface cores analysed
Laguna Azul	14°59'27"	64°48'45"	Seasonally-inundated savanna	2006	3
Laguna Belen	14°27'18"	64°51'30"	Seasonally-inundated savanna	2006	3
Laguna Suarez	14°52'51"	64°51'59"	Seasonally-inundated savanna	2006	3
Laguna Cernandez	14°41'18"	64°45'55"	Seasonally-inundated savanna	2006	3
Laguna Coitarama	14°30'10"	54°51'39"	Seasonally-inundated savanna	2006	3
Laguna Socorros	16°08'	63°07'	SDTF	2002	1
Laguna Mandioré	18°05'	57°33'	Seasonally-inundated savanna / SDTF	2001	3
Laguna La Gaiba	17°47'	57°43'	Seasonally-inundated savanna / SDTF	2001	4

Table 3.2. Location of lakes sampled for their modern pollen rain.

3.2.3. Vegetation sampling

Various savanna and SDTF sites were sampled within Noel Kempff Mercado National Park, Bolivia by Tim Killeen (Museo de Natural Historia, Santa Cruz, Bolivia) and co-workers. Full sampling details are available on the SALVIAS database (SALVIAS, 2008) and are summarised in below.

For the SDTF sites, one hectare of forest was sampled and all freestanding plants (lianas were excluded) with a diameter at breast height (dbh) greater than 10 cm at 1.4 m above ground level, or above buttresses, were registered. The savanna vegetation was sampled using a point intercept methodology. A 500 m baseline was

marked at each site and between nine and fifteen 20 m lines were selected perpendicular to this baseline. The horizontal coverage (the amount of ground cover by each individual along the line transect) of each plant along these 20 m lines was recorded, yielding a total linear coverage of 180 to 300 m for each site.

3.3. Laboratory methods

The method for the preparation of pollen traps was adapted from Gosling *et al.* (2003) with modifications by Michael Burn (pers. com) and the author. Lake sediment samples were prepared using standard methods adapted from Faegri & Iverson, (1989) and Moore *et al.* (1991). To allow pollen influx values to be calculated a number of exotic *Lycopodium* marker pollen tablets were added to each sample during processing (Stockmarr, 1971).

3.3.1. Procedure for pollen processing of funnel trap samples with viscose rayon fibre

List of chemicals (per sample)

5% Sodium pyrophosphate: ca 100-150 ml
3-6 *Lycopodium* tablets
10% hydrochloric acid: 30 ml in total
40% hydrofluoric acid: 20 ml
Glacial acetic acid: 20 ml in total
Concentrated sulphuric acid: 1 ml
Acetic anhydride: 9 ml
Tertiary butyl alcohol (TBA): 8 ml
Silicone oil: ca 3-4 ml dependant on sample concentration

Pollen concentration

1. Add 5% sodium pyrophosphate dispersant to the plastic bags containing the viscose rayon pad. This should be enough to fully saturate the sample. The sample is then left overnight to allow pollen to be freed from the fibres.

2. Dissolve *Lycopodium* marker tablets in 10 ml of 10% hydrochloric acid, add to the plastic bag and massage thoroughly to ensure that the contents are well mixed.

3. Top-up the plastic bag with distilled water, massage thoroughly and pass the sample through a 250 µm sieve into a large beaker. The rayon pad will remain in the sieve and should be continually washed in distilled water and massaged until approximately 2000 ml of liquid is retrieved.

4. Pour the remaining liquid into a practical number of 50 ml centrifuge tubes and centrifuge the samples for 3 minutes at 4000 rpm. Decant the supernatant for each of the centrifuge tubes and retain the pellet of material at the base. Once all the water is decanted transfer the pellets into one 50 ml centrifuge tube.

HF acid treatment

1. In a fume cupboard, add 20 ml of 40% hydrofluoric acid to the sample. Mix well with a polypropylene rod. The sample is left in boiling water bath for 15 minutes. Stir occasionally.

2. Centrifuge the sample for 3 minutes at 4000 rpm and decant the supernatant.

3. Add 20 ml of 10% HCl, stir and heat in a boiling water bath for 20-30 minutes to remove any fluorosilicate residues, stirring occasionally. Centrifuge and decant the supernatant.

4. Wash sample with distilled water. Centrifuge and decant.

Acetolysis

1. Wash the sample with 10 ml glacial acetic acid and mix well. Centrifuge and decant.

2. Make up the acetolysis solution in a 100 ml measuring cylinder: 1 part concentrated sulphuric acid added to 9 parts acetic anhydride. Add sulphuric acid slowly since the reaction is very exothermic. Add 10 ml to the sample, mix well with a polypropylene rod and heat in a boiling water bath for 3 minutes stirring occasionally. Centrifuge and decant.

3. Wash with 10 ml glacial acetic acid, mix well, centrifuge and decant.

4. Wash with distilled water, centrifuge and decant.

5. Transfer to 15 ml centrifuge tubes, centrifuge and decant again.

Silicone oil mounting

1. Wash the sample with 3 to 4 ml of TBA, having warmed the TBA to melting point in a water bath, mix well, centrifuge and decant.

2. Repeat above stage to ensure through dehydration.

3. Add silicone oil (3 times the volume of the remaining pellet) and stir very well using stir stick.

4. Place the open tube in a drying rack at 60^{o}C for around 48 hours or until bubbles of TBA are no longer visible. Stir at least once a day.

Slide preparation

1. Place a beaker of paraffin wax on a hot plate adjusted to around 60^{o}C – enough to ensure the wax just melts.

2. Stir sample once again to ensure that pollen is thoroughly mixed in the silicone oil.

3. Add a drop of sample onto a slide using a stir stick.

4. Place the slide onto the hot plate and wait until the air bubbles have disappeared.

5. Place cover slip over the slide and add the melted paraffin wax to the perimeter of the cover slip in order to seal the sample.

6. Remove slide from hot plate and allow wax to harden

7. Clear nail varnish may then be used to seal the slide.

3.3.2. Procedure for pollen processing of sediment samples

List of chemicals (per sample)

10% KOH or NaOH: 6 ml
2 *Lycopodium* tablets
10% hydrochloric acid: 9 ml
40% hydrofluoric acid: 5 ml
Glacial acetic acid: 10 ml
Concentrated sulphuric acid: 0.5 ml
Acetic anhydride: 4.5 ml

Tertiary butyl alcohol (TBA): 8 ml

Silicone oil: ca 3-4 ml dependant on sample concentration

Sample: 1 cubic centimetre

Sample measurement and removal of carbonates

1. Place 1 cm^3 of sample in a small 15 cm^3 measuring cylinder containing 3 ml of 10% HCl, until the liquid level rises to 4 ml. If no reaction then sample is free from carbonates.

Absolute pollen techniques

1. Add 2 *Lycopodium* tablets to the centrifuge tube, adding 10% HCl up to the 10 ml mark, stir gently until dissolved.

2. Centifuge and decant.

Potassium hydroxide digestion

1. Add 6 ml of 10% KOH or NaOH to the sample and place in a boiling water bath for 10-15 minutes stirring occasionally.

2. Wash 2-3 times with distilled water until no trace of brown colour remains in the supernatant, remembering to mix thoroughly each time after decanting.

3. Pass the sample through a sieve (250 µm), placed in a funnel which leads into a clean 50 ml centrifuge tube to allow pollen and spores to pass through, whilst retaining the courser material, such as sand and plant debris.

4. Decant between beakers if an obvious fine sand fraction remains.

5. Balance the tubes with distilled water, centrifuge and decant.

HF acid treatment

1. In a fume cupboard, add 5 ml of 40% hydrofluoric acid to the sample. Mix well with a polypropylene rod. The sample is placed in a boiling water bath for 15 minutes or more. Stir occasionally.

2. Centrifuge the sample for 3 minutes at 4000 rpm and decant the supernatant.

3. It may be necessary to repeat stage 1 and 2 one or more times if the sample is very minerogenic.

4. Add 6 ml of 10% HCl, stir and heat in a boiling water bath for 20-30 minutes to remove any fluorosilicate residues, stirring occasionally. Centrifuge and decant the supernatant.

5. Wash sample with distilled water, centrifuge and decant.

Acetolysis

1. Wash the sample with 5 ml glacial acetic acid and mix well, centrifuge and decant.

2. Make up the acetolysis solution in a 100 ml measuring cylinder: 1 part concentrated sulphuric acid added to 9 parts acetic anhydride. Add sulphuric acid slowly since the reaction is very exothermic. Add 5 ml to the sample, mix well with a polypropylene rod and heat in a boiling water bath for 3 minutes stirring occasionally. Centrifuge and decant.

3. Wash with 5 ml glacial acetic acid, mix well, centrifuge and decant.

4. Wash with distilled water, centrifuge and decant.

5. Transfer to 15 ml centrifuge tubes, centrifuge and decant again.

Silicone oil mounting and slide preparation followed the same procedure as outlined in section 3.3.1.

3.3.3. Preparation of pollen reference material

Flowers of neotropical plant taxa were obtained from herbarium material at the Royal Botanic Gardens, Edinburgh, UK and the Museo de Natural Historia, Santa Cruz, Bolivia to obtain reference material to improve the identification of unknown pollen grains. The samples were prepared using a procedure modified from the standards methods of Faegri & Iverson (1989) and Moore *et al.* (1991).

List of chemicals (per sample)

10% KOH or NaOH: 7 ml
Glacial acetic acid: 10 ml
Concentrated sulphuric acid: 0.5 ml
Acetic anhydride: 4.5 ml
Tertiary butyl alcohol (TBA): about 10 ml
Silicone oil: ca 3-4 ml dependant on sample concentration

1. Place whole flower(s) into centrifuge tube.

2. Add 7 ml 10% KOH or NaOH. Heat in boiling water bath for 5 minutes. Sieve to remove large organics (250 µm sieve). Rinse centrifuge tube with distilled water. Return sample to centrifuge tube. Centrifuge and decant.

3. Wash with 5 ml distilled water. Centrifuge and decant.

Acetolysis

1. Wash the sample with 5 ml glacial acetic acid and mix well. Centrifuge and decant to pollen waste.

2. Make up the acetolysis solution in a 100 ml measuring cylinder: 1 part concentrated sulphuric acid added to 9 parts acetic anhydride. Add 5ml to the sample, mix well with a polypropylene rod and heat in a boiling water bath for 3 minutes stirring occasionally. Centrifuge and decant to pollen waste.

3. Wash with 5 ml glacial acetic acid, mix well, centrifuge and decant.

4. Wash with distilled water, centrifuge and decant.

Silicone oil mounting and slide preparation followed the same procedure as outlined in section 3.3.1.

3.3.4. Pollen processing of surface soil samples

As several of the artificial pollen traps from the savanna ecosystems were damaged by fire, it was decided to process surface soils sample from one of the savanna sites (FC1) to investigate whether this was a feasible method of analysing the modern pollen rain of the ecosystem and to augment the limited number of pollen traps available from this site. The soil samples were collected from the soil surface of the sites once any leaf litter had been removed. Various research has shown the feasibility of using surface soil sediments to obtain the modern pollen rain of an ecosystem from both high latitudes and tropical regions (Dimbleby, 1957; Reese and Liu, 2005). However, there are considerable problems with using soil samples for pollen analysis and these are associated with poor pollen preservation and vertical mixing within the soil profile (Birks and Birks, 1980).

The laboratory method for the preparation of soil samples was the same as that listed in section 3.3.2. However, the preparations contained very few pollen grains and the pollen grains that were present were in a poor state of preservation, hence it was decided that it would not be feasible to use surface soils samples as a method of analysing the modern pollen rain from savanna sites.

3.4. Pollen counting

Due to the high species diversity of tropical ecosystems there has been uncertainty about the pollen sum required to capture this biodiversity. Counts of approximately 300 pollen grains per pollen trap were adopted for this study as this count size allowed the major taxa (those with a percentage >1%) to be observed. It was noted that any additional taxa encountered beyond this sum size occurred at very low percentages (<1%) and were usually weakly sculptured (psilate or scabrate) tricolporate grains whose morphological features did not allow them to be reliably identified to any specific taxonomic group. Hence, it is considered that the sum size was sufficiently large to capture the key taxa within the modern pollen rain of the ecosystem. For the surface lake sediments, a pollen sum of approximately 300 pollen grains per sample was used with aquatic taxa excluded from the sum.

Four pollen traps per year for each site were counted where possible, the exceptions being the sites which had a poor return of pollen traps due to damage by fire/animals. The upland savanna site (FC1) had poor pollen trap recovery rate as all samples from the 2000 sampling year had been severely damaged by fire; hence 12 traps were counted from this site from the 1999 and 2001 sampling years only. For the seasonally-inundated SDTF (MV1) site, four traps were counted from the 1999 sampling year, three from the 2000 sampling year and five traps from the 2001 sampling year.

Pollen was identified using an Olympus BX40 light microscope at x 400 and x 1000 magnification. Pollen was identified using Roubik and Moreno (1991), Colinvaux *et*

al. (1999), Salgado-Labouriau (1973) and the modern pollen reference collection of neotropical pollen at the University of Edinburgh. The pollen counts were then converted to percentage data and plotted as stratigraphic diagrams using the C2 version 1.5 software package (Juggins, 2003).

3.4.1. Moraceae/Urticaceae pollen differentiation

Recent research (Burn and Mayle, 2008) has outlined the potential for differentiating pollen from the Moraceae/Urticaceae taxonomic group. Although the Moraceae and Urticaceae families are predominately evergreen forest species within NKMNP (Killeen and Schulenberg, 1998), some species of Moraceae can be found within the savanna ecosystems of NKMNP (e.g. *Brosimum gaudichaudii* and *Sorocea guilleminiana).* In response to this advance in the pollen taxonomy, it was decided to perform selected identifications of Moraceae/Urticaceae grains within the pollen traps from NKMNP, with the aim to estimate the proportion of Moraceae/Urticaceae pollen that was of a "regional" nature (i.e. from Moraceae/Urticaceae species that are representative of evergreen forest ecosystems and are absent from savanna/SDTF ecosystems in NKMNP) and to estimate the proportion of Moracae/Urticaceae pollen which may be derived from species growing within the vegetation plot i.e. of a "local", savanna origin.

Fifty Moraceae/Urticaceae pollen grains were counted from six traps from each ecosystem. The level of differentiation is not as great as that described by Burn and Mayle (2008) as imperfect preservation of Moraceae/Urticaceae pollen within the pollen traps made it very difficult to differentiate the taxa with small diporate pollen (e.g. *Maclura* spp.*, Coussapoa* spp.*, Pilea* spp.*, Sorocea* spp.) and these pollen grains were grouped into a Moraceae/Urticaceae undifferentiated category. Also included in this group were pollen grains that were identifiable as Moraceae/Urticaceae, however imperfect preservation prevented the grain being identified to a lower taxonomic level.

3.5. Summary of chapter

This chapter outlines the two methods (artificial pollen traps and surface lake sediments) used to capture the modern pollen rain from the study sites and the strategy that was used to sample the vegetation of the savanna and SDTF sites. The laboratory protocols for extracting the pollen grains from these samples were also described, along with the pollen counting methodology. The following chapter analyses the vegetation data collected from the study sites to investigate the floristic differences between the different types of savanna and SDTF using inundation regime as the key separating environmental factor. Chapter 5 then combines the vegetation data with the modern pollen rain data from the study sites to allow the ecosystems to be characterised by their modern pollen rain and to investigate the pollen production of different types of vegetation present in the study sites. Chapter 6 attempts to differentiate the ecosystems by their modern pollen rain.

Chapter 4. Floristic differentiation of savanna and seasonally dry tropical forests in NE Bolivia

Contents

4.1. Introduction to chapter *59*

4.2. Study sites and the ecology of neotropical savannas and seasonally dry forests *59*

4.3. Methods *60*

4.3.1. Vegetation sampling 60

4.3.2. Statistical methods 61

4.4. Results *66*

4.4.1. Dominant taxa 66

4.4.2. Results for savanna ordinations 66

4.4.3. Results of forest ordinations 66

4.5. Discussion *82*

4.5.1. Savanna sites 82

4.5.2. SDTF sites 84

4.6. Conclusions *86*

4.7. Summary of chapter *87*

4.1. Introduction to chapter

The aim of this chapter is to investigate the floristic differences of savanna and dry forest ecosystems in the vicinities of Noel Kempff Mercado National Park in eastern Bolivia. Most research on the floristics of seasonally dry tropical forest (SDTF) and savanna ecosystems has concentrated on trying to detect the floristic similarities between different geographical regions of one ecosystem (e.g. Ratter *et al.,* 2003, Killeen *et al.,* 2006). This research will attempt to investigate the floristic differences between different ecosystems within the same geographical region using the inundation regime (seasonal-inundation versus no inundation) as the key environmental variable under consideration. The results of this study will be used to enhance our understanding of the current ecological preferences of taxa present in the SDTF and savanna ecosystems. Another application is to identify taxa that are diagnostic for the differentiation of these ecosystems. This will assist the identification of pollen taxa that could have importance for differentiating these ecosystems by their modern pollen rain (discussed in chapter 6), as the modern pollen rain of an ecosystem is a function of its vegetation. It is anticipated that these findings will be relevant for the interpretation of fossil pollen records from the Neotropics.

4.2. Study sites and the ecology of neotropical savannas and seasonally dry forests

The study site is Noel Kempff Mercado National Park, Bolivia (see chapter 2 for detailed description of this locality). The ecosystems under consideration in this chapter are upland savannas, seasonally-inundated savannas, upland SDTF and seasonally-inundated SDTF. The ecology of these ecosystems is discussed fully in chapter 2.

4.3. Methods

Vegetation plot data were obtained from the SALVIAS database (SALVIAS, 2008). Plots were obtained for nine savanna sites (encompassing five upland savanna plots and four lowland seasonally-inundated plots) and six forest plots (four upland SDTF plots, one seasonally-inundated SDTF plot and one semi-deciduous palm forest plot).

4.3.1. Vegetation sampling

Full sampling details are available on the SALVIAS database (SALVIAS, 2008) and are summarised in chapter 3. Locations and descriptions of the plots are listed in tables 4.1 and 4.2, and figure 4.1.

The raw botanical inventory data obtained from the SALVIAS database (SALVIAS, 2008) was then processed so that the attributes, % of total stems and % of total basal area, were calculated at the family, genus and species level for the forest data using equations 4.1 and equation 4.2.

$$\% \text{ of total stems} = \frac{\text{Number of individuals of a taxon}}{\text{Total number of individuals of all taxa}} \times 100$$

Equation 4.1. Formula to calculate % of total stems.

$$\% \text{ of total basal area} = \frac{\text{Combined basal area of a taxon}}{\text{Total basal area of all taxa}} \times 100$$

Equation 4.2. Formula to calculate % of total basal area.

As the vegetation sampling method was different for the savanna plots (all plants sampled using a line transect methodology) compared to the forest plots (only those plants with a dbh ≥10 cm sampled), the attributes relative cover and relative frequency were calculated at family genus and species level for the savanna data (equation 4.3 and equation 4.4).

$$\text{Relative frequency} = \frac{\text{Total number of individuals of a taxon}}{\text{Total number of individuals of all taxa}} \times 100$$

Equation 4.3. Formula to calculate relative frequency.

$$\text{Relative cover} = \frac{\text{Total horizontal coverage of a taxon}}{\text{Total horizontal coverage of all taxa}} \times 100$$

Equation 4.4. Formula to calculate relative cover.

4.3.2. Statistical methods

To investigate the floristic similarity between the different ecosystems, ordination methods were used. Ordination is a multivariate data analysis technique that aims to present different sites in a two-dimensional space so that sites with a high degree of similarity plot close to each other, whilst those sites with a high degree of dissimilarity plot far apart from each other (ter Braak, 1995). In this research, the (dis)similarity is based upon the taxonomic composition of the sites. Due to the different vegetation sampling methods (see above) it was not possible to ordinate the savanna and SDTF plots together, hence the savanna data and the forest data were used in separate ordinations. Criteria outlined in ter Braak (1995) were used to decide which ordination method was applicable to the datasets. The gradient lengths of the datasets were investigated using detrended correspondence analysis (DCA) and were found to be intermediate between those which suggest the use of principal components analysis (PCA) and those which suggest the use of DCA. Therefore, it was decided to ordinate the data with both methods. As the results were similar, it was decided to select PCA over DCA due to its relative simplicity (Birks and Gordon, 1985).

Prior to the ordination, the data were square-root transformed as recommended for percentage data (Birks, 1986; Prentice, 1986) to reduce the variance within the dataset and hence to reduce the influence of dominant taxa. The ordinations were performed using the C2 version 1.5 software package (Juggins, 2003) and the

Community Ecology Package version 1.8-5 (Oksanen *et al.,* 2007) available as freeware in R (R Development Core Team, 2007).

For the savanna ordinations, the relative cover data was used and for the SDTF ordinations the % of total basal area data was used. The ordinations were performed at genus level and family level. It was decided not to ordinate the data at species level for the following reasons; (i) there are a high number of species within the datasets that were only identified to genus level, hence an analysis at species level would have included numerous undetermined species; (ii) to enhance the applicability of the finding to palaeoecologists who often use pollen analysis as a method to infer former vegetation assemblages. Pollen taxonomic resolution is low compared with botanical identifications and it is very difficult to identify many pollen grains to species level; and (iii) some species have small geographical ranges so could possibly only be found within one inventory and are therefore only representative of a small geographic area (ter Steege *et al.,* 2006).

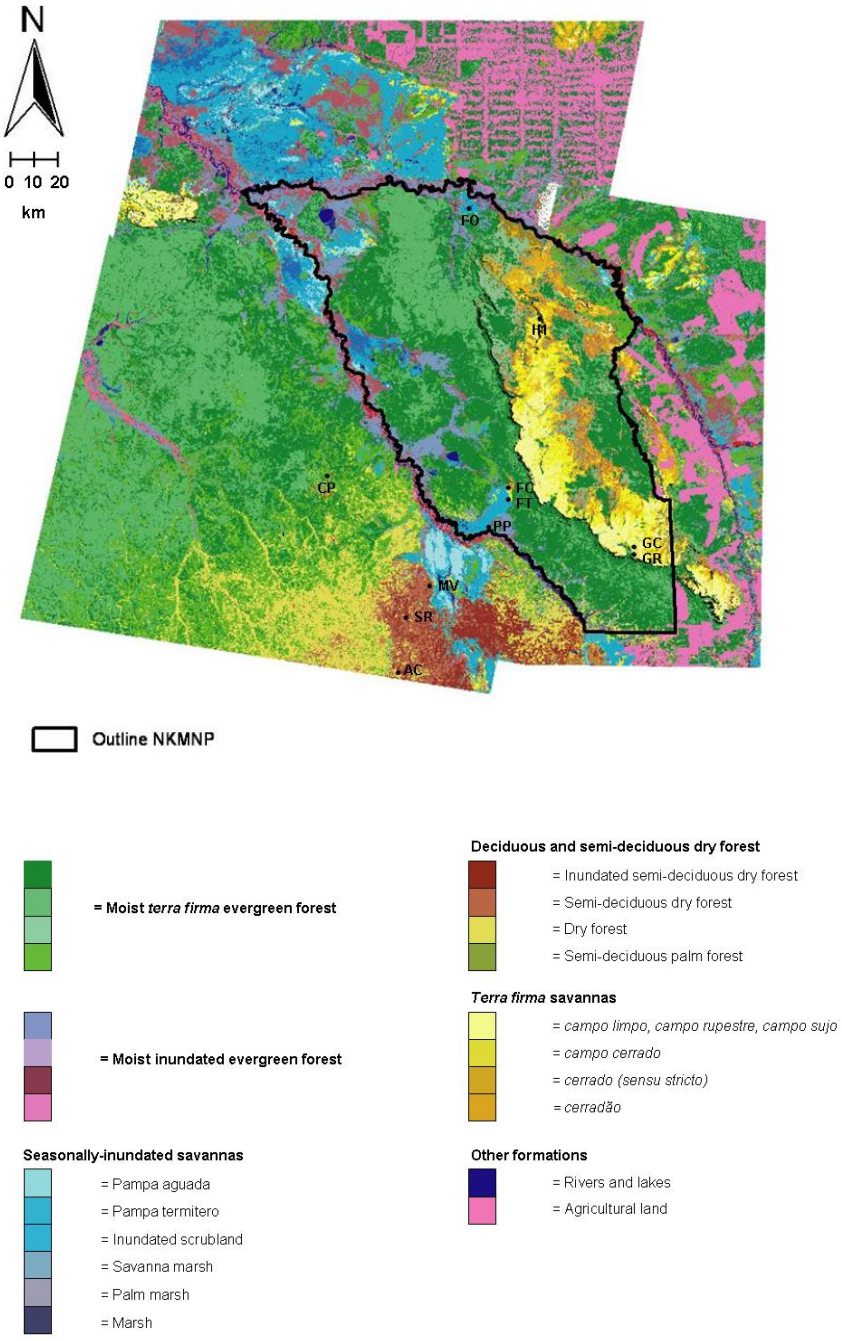

Figure 4.1. Location of vegetation plots within NKMNP, Bolivia (modified from Killeen and Schulenberg, 1998).

Plot	Latitude (S)	Longitude (W)	Site name	Ecosystem	Substrate	Slope (degrees)	Inundation regime	Altitude (m)
AC1	15°14'46"	61°14'34"	Acuario	Semi-deciduous forest	Granitic	0	Xeric	300
AC2	15°14'46"	61°14'34"	Acuario	Semi-deciduous forest	Granitic	0	Xeric	300
CP1	14°32'28"	61°29'53"	Cerro Pelao	Deciduous forest	Granitic	20	Xeric	400
CP2	14°32'16"	61°30'02"	Cerro Pelao	Deciduous forest	Granitic	20	Xeric	400
MV1	14°56'27"	61°07'59"	Monte Verde	Seasonally-inundated semi-deciduous forest	Quaternary sediments	0	Seasonal	230
SR1	14°59'59"	61°13'17"	San Roque	Semi-deciduous palm forest	Quaternary sediments	0	Mesic	300

Table 4.1. Environmental attributes of the forest ecosystems within NKMNP (Panfil, 2001). A detailed description of the vegetation physiognomies is provided in chapter three.

Plot	Latitude (S)	Longitude (W)	Site name	Ecosystem	Substrate	Slope (degrees)	Inundation depth	Altitude (m)
FC1	14 °36'25"	60 °51'23"	Los Fierros	*Cerrado*	Tertiary laterite	0	None	200
FC2	14 °34'45"	60 °50'29"	Los Fierros	*Cerradão*	Granitic	<1	None	200
FO1	13 °32'41"	61 °01'23"	Flor de Oro	Termite savanna	Quaternary Sediments	0	~30 cm	120
FO2	13 °33'50"	61 °01'02"	Flor de Oro	Termite savanna	Quaternary Sediments	0	~30 cm	120
FT	14 °36'53"	60 °51'59"	Los Fierros	Termite savanna	Quaternary sediments	0	~30 cm	200
GC	14 °48'11"	60 °23'33"	Las Gamas	*Cerrado*	Sandstone	<1	none	850
GR	14 °48'11"	60 °23'33"	Las Gamas	*Campo rupestre*	Quartzite	<1	none	900
H1	13 °53'55"	60 °48'46"	Huanchaca	*Campo sujo*	Tertiary Laterite	<1	none	550
PP	14 °44'37"	60 °57'38"	Puerto Pasto	*Pampa inundada*	Quaternary Sediments	0	1-2 m	200

Table 4.2. Environmental attributes of the savanna ecosystems within NKMNP (Panfil, 2001). A detailed description of the vegetation physiognomies is provided in chapter three.

4.4. Results

4.4.1. Dominant taxa

The top five families, genera and species at each site are displayed in tables 4.3 to 4.17.

4.4.2. Results for savanna ordinations

For the family plot (figure 4.2), the first two axes represent 48.48% of the variance (λ_1 = 29.58% and λ_2 = 18.90%). The key taxa (those with the highest magnitude taxon scores on PCA axes 1 and 2) are shown in table 4.18. For the genus plot (figure 4.3), the first two axes represent 41.17% of the variance (λ_1 = 21.71% and λ_2 = 19.46%). The key taxa (those with the highest magnitude taxon scores on PCA axes 1 and 2) are shown in table 4.19. Both the family level ordination and the genus level ordination show a similar pattern with Axis 1 separating the upland savanna (cerrado) sites (FC1, FC2, H1, GR) from the other sites (FO1, FO2, FT and GR). Axis 2 separates the PP (inundated grassland site) from the rest of the sites. The *campo rupestre* site (GR) plots with the lowland seasonally-inundated sites. The remaining taxon scores and eigenvectors are presented in the appendix.

4.4.3. Results of forest ordinations

For the family plot (figure 4.4), the first two axes represent 76.54% of the variance (λ_1 = 47.25% and λ_2 = 29.29%). The key taxa (those with the highest magnitude taxon scores on PCA axes 1 and 2) are shown in table 4.20. For the genus plot (figure 4.5), the first two axes represent 66.87% of the variance (λ_1 = 35.62% and λ_2 = 31.25%). The key taxa (those with the highest magnitude taxon scores on PCA axes 1 and 2) are shown in table 4.21. Both the family level ordination and the genus level ordination show very similar patterns with the negative side of PCA axis 1 containing the four upland SDTF sites (AC1, AC2, CP1, CP2) and the positive side

of this axis containing the semi-deciduous palm forest (SR1) site. The inundated SDTF (MV1) site plots separately. The remaining taxon scores and eigenvectors are presented in the appendix.

Family – AC1	% of total stems	% of total basal area	Genus	% of stems	% of total basal area	Species	% of total stems	% of total basal area
Fabaceae	20.37	31.07	*Tabebuia*	13.03	9.91	*Simira cordifolia*	9.72	3.67
Bignoniaceae	17.43	11.06	*Simira*	9.72	3.67	*Casearia gossypiosperma*	8.44	3.97
Rubiaceae	9.91	3.68	*Casearia*	9.36	4.34	*Tabebuia roseo-alba*	7.34	4.00
Flacourtiaceae	9.36	4.34	*Pseudobombax*	6.42	12.29	*Pseudobombax marginatum*	6.42	12.29
Bombacaceae	8.81	14.92	*Anadenanthera*	5.50	11.67	*Tabebuia impetiginosa*	5.69	5.91

Table 4.3. Percentage of stems and percentage of total basal area for family, genus and species at the AC1 site.

Family – AC2	% of total stems	% of total basal area	Genus	% of total stems	% of total basal area	Species	% of total stems	% of total basal area
Fabaceae	31.98	38.29	*Caesalpinia*	11.56	17.02	*Caesalpinia floribunda*	11.56	17.02
Bignoniaceae	10.98	6.91	*Casearia*	8.48	3.38	*Tabebuia roseo-alba*	7.32	5.74
Flacourtiaceae	8.86	3.42	*Tabebuia*	8.09	6.01	*Anadenanthera colubrina*	6.94	13.39
Arecaceae	5.59	12.72	*Anadenanthera*	6.94	13.39	*Casearia gossypiosperma*	6.17	2.63
Combretaceae	5.59	3.84	*Combretum*	5.59	3.84	*Combretum leprosum*	5.59	3.84

Table 4.4. Percentage of stems and percentage of total basal area for family, genus and species at the AC2 site.

Family – CP1	% of total stems	% of total basal area	Genus	% of total stems	% of total basal area	Species	% of total stems	% of total basal area
Fabaceae	20.32	23.85	*Combretum*	17.30	13.16	*Combretum leprosum*	16.98	13.11
Combretaceae	17.46	13.16	*Aspidosperma*	14.92	15.84	*Aspidosperma cylindrocarpon*	9.05	9.51
Apocynaceae	14.92	15.84	*Anadenanthera*	7.94	14.16	*Anadenanthera colubrina*	7.94	14.16
Anacardiaceae	8.73	12.10	*Luehea*	7.62	3.64	*Luehea candicans*	7.62	3.64
Tiliaceae	7.62	3.64	*Spondias*	6.19	9.86	*Spondias mombin*	6.19	9.86

Table 4.5. Percentage of stems and percentage of total basal area for family, genus and species at the CP1 site.

Family – CP2	% of total stems	% of total basal area	Genus	% of total stems	% of total basal area	Species	% of total stems	% of total basal area
Meliaceae	13.97	2.63	*Trichilia*	13.97	2.63	*Trichilia elegans*	12.59	2.51
Fabaceae	13.63	15.73	*Combretum*	9.88	12.46	*Combretum leprosum*	9.52	12.45
Combretaceae	10.39	12.55	*Simira*	5.96	3.28	*Simira* sp.	5.95	3.28
Flacourtiaceae	6.47	3.01	*Casearia*	5.62	2.87	*Talisia esculenta*	4.25	2.66
Rubiaceae	6.13	3.38	*Talisia*	4.26	2.66	*Spondias mombin*	4.08	12.94

Table 4.6. Percentage of stems and percentage of total basal area for family, genus and species at the CP2 site.

Family – MV1	% of total stems	% of total basal area	Genus	% of total stems	% of total basal area	Species	% of total stems	% of total basal area
Fabaceae	19.40	20.41	*Physocalymma*	13.43	19.47	*Physocalymma scaberrimum*	13.43	19.47
Lythraceae	13.43	19.47	*Hirtella*	13.09	15.57	*Hirtella gracilipes*	13.09	15.57
Chrysobalanaceae	13.09	15.57	*Inga*	10.56	10.35	*Inga ingoides*	7.23	5.02
Moraceae	8.84	6.19	*Sorocea*	4.36	0.32	*Sorocea guilleminiana*	4.36	0.32
Annonaceae	3.79	1.38	*Xylopia*	3.67	1.33	*Xylopia sericea*	3.33	1.27

Table 4.7. Percentage of stems and percentage of total basal area for family, genus and species at the MV1 site.

Family – SR1	% of total stems	% of total basal area	Genus	% of total stems	% of total basal area	Species	% of total stems	% of total basal area
Arecaceae	54.00	84.28	*Orbignya*	50.80	83.46	*Orbignya phalerata*	50.80	83.46
Fabaceae	10.66	3.65	*Astronium*	6.75	4.75	*Machaerium acutifolium*	4.09	1.65
Anacardiaceae	7.46	5.07	*Machaerium*	4.80	1.83	*Luehea candicans*	3.55	0.44
Tiliaceae	3.91	0.44	*Luehea*	3.55	0.44	*Astronium lecointei*	3.37	0.33
Bignoniaceae	3.37	0.57	*Tabebuia*	3.37	0.57	*Astronium urundeuva*	3.37	4.42

Table 4.8. Percentage of stems and percentage of total basal area for family, genus and species at the SR1 site.

Family – FO1	Relative cover	Relative frequency	Genus	Relative cover	Relative frequency	Species	Relative cover	Relative frequency
Poaceae	81.46	84.69	*Paspalum*	24.35	30.57	*Paspalum lineare*	20.34	23.37
Araliaceae	2.53	0.34	*Andropogon*	19.93	16.00	*Andropogon virgatus*	19.64	15.54
Apocynaceae	2.53	0.40	*Axonopus*	17.72	14.80	*Axonopus pulcher*	16.38	12.74
Polygalaceae	2.25	1.31	*Schizachyrium*	7.15	6.69	*Schizachyrium sanguineum*	6.70	6.06
Myrtaceae	1.53	0.51	*Panicum*	2.72	0.86	*Paspalum plicatulum*	4.01	7.20

Table 4.9. Relative cover and relative frequency for family, genus and species at the FO1 site.

Family – FO2	Relative cover	Relative frequency	Genus	Relative cover	Relative frequency	Species	Relative cover	Relative frequency
Poaceae	69.55	73.70	*Elyonurus*	21.93	12.08	*Elyonurus muticus*	21.93	12.08
Lauraceae	4.38	0.20	*Schizachyrium*	16.07	22.57	*Schizachyrium sanguineum*	16.07	22.57
Dilleniaceae	3.30	0.64	*Andropogon*	7.66	3.63	*Andropogon selloanus*	7.62	3.56
Flacourtiaceae	2.96	1.39	Poaceae gen_indet.p10	6.92	7.40	Poaceae gen_indet. pasto10	6.92	7.40
Cyperaceae	2.84	7.30	*Axonopus*	6.32	8.99	*Ocotea aciphylla*	4.38	0.20

Table 4.10. Relative cover and relative frequency for family, genus and species at the FO2 site.

Family – FC1	Relative cover	Relative frequency	Genus	Relative cover	Relative frequency	Species	Relative cover	Relative frequency
Poaceae	51.01	68.74	*Paspalum*	22.11	34.91	*Andropogon virgatus*	12.43	17.83
Fabaceae	5.61	3.78	*Andropogon*	12.43	17.83	*Paspalum pectinatum*	10.57	11.41
Rubiaceae	5.10	3.78	*Elyonurus*	10.35	6.48	*Elyonurus muticus*	10.35	6.48
Myrtaceae	5.01	5.27	*Borreria*	4.88	3.17	*Paspalum stellatum*	9.82	20.86
Dilleniaceae	3.85	2.03	*Davilla*	3.79	1.96	*Borreria* sp.1	4.88	3.17

Table 4.11. Relative cover and relative frequency for family, genus and species at the FC1 site.

Family – FC2	Relative cover	Relative frequency	Genus	Relative cover	Relative frequency	Species	Relative cover	Relative frequency
Poaceae	51.01	78.84	*Trachypogon*	22.56	42.09	*Trachypogon plumosus*	22.56	42.09
Clusiaceae	20.34	2.60	*Caraipa*	19.88	2.20	*Caraipa densifolia*	19.88	2.20
Fabaceae	4.73	2.47	Poaceae gen_indet.sp11	16.49	18.87	Poaceae gen_indet. sp.11	11.79	9.27
Melastomataceae	3.18	3.31	*Paspalum*	4.65	7.59	Poaceae gen_indet. sp.5	4.42	8.69
Bombacaceae	2.21	0.39	*Sporobolus*	2.76	3.37	*Paspalum pectinatum*	3.00	4.80

Table 4.12. Relative cover and relative frequency for family, genus and species at the FC2 site.

Family - FT	Relative cover	Relative frequency	Genus	Relative cover	Relative frequency	Species	Relative cover	Relative frequency
Poaceae	74.93	53.47	*Paspalum*	28.23	18.13	*Paspalum lineare*	21.50	13.18
Cyperaceae	7.13	18.75	*Mesosetum*	14.59	13.18	*Mesosetum cayennense*	14.59	13.18
Eriocaulaceae	2.71	7.55	*Elyonurus*	11.68	4.33	*Elyonurus muticus*	11.68	4.33
Xyridaceae	1.89	6.75	*Andropogon*	6.13	4.46	*Andropogon lateralis*	5.53	4.02
Malpighiaceae	1.40	0.50	*Leptocoryphium*	5.17	1.55	*Leptocoryphium lanatum*	5.17	1.55

Table 4.13. Relative cover and relative frequency for family, genus and species at the FT site.

Family – H1	Relative cover	Relative frequency	Genus	Relative cover	Relative frequency	Species	Relative cover	Relative frequency
Poaceae	57.76	66.94	*Paspalum*	24.49	22.53	*Paspalum pectinatum*	23.13	18.79
Dilleniaceae	6.16	2.68	*Elyonurus*	17.65	19.68	*Elyonurus muticus*	17.65	19.68
Ochnaceae	4.21	3.33	*Davilla*	6.16	2.68	*Davilla grandiflora*	5.79	2.56
Fabaceae	4.05	4.82	*Andropogon*	4.36	8.09	*Andropogon virgatus*	4.36	8.09
Rubiaceae	3.27	1.84	*Ouratea*	4.21	3.33	*Ouratea* sp.1	3.16	2.38

Table 4.14. Relative cover and relative frequency for family, genus and species at the H1 site.

Family – GC	Relative cover	Relative frequency	Genus	Relative cover	Relative frequency	Species	Relative cover	Relative frequency
Poaceae	42.24	66.92	*Axonopus*	24.23	38.68	*Axonopus fissifolius*	16.02	31.31
Melastomataceae	4.66	2.02	*Thrasya*	9.70	10.23	*Thrasya petrosa*	9.70	10.23
Malpighiaceae	4.45	1.05	*Miconia*	4.47	1.64	*Axonopus pulcher*	6.57	5.81
Myrtaceae	3.94	2.06	*Ilex*	3.93	1.98	*Ilex inundata*	3.93	1.98
Aquifoliaceae	3.93	1.98	*Paspalum*	3.74	9.22	*Miconia macrothyrsa*	3.56	0.88

Table 4.15. Relative cover and relative frequency for family, genus and species at the GC site.

Family - GR	Relative cover	Relative frequency	Genus	Relative cover	Relative frequency	Species	Relative cover	Relative frequency
Poaceae	81.34	81.61	*Axonopus*	39.88	34.53	*Axonopus canescens*	31.88	19.66
Velloziaceae	10.80	6.55	*Leptocoryphium*	21.13	20.93	*Leptocoryphium lanatum*	21.13	20.93
Fabaceae	3.21	4.02	*Vellozia*	10.79	6.55	*Vellozia flavicans*	10.79	6.56
Cyperaceae	1.25	2.81	*Elyonurus*	9.77	6.17	*Elyonurus muticus*	9.77	6.17
Euphorbiaceae	0.53	0.94	*Andropogon*	2.25	5.56	*Axonopus stolons*	6.46	12.72

Table 4.16. Relative cover and relative frequency for family, genus and species at the GR site.

Family - PP	Relative cover	Relative frequency	Genus	Relative cover	Relative frequency	Species	Relative cover	Relative frequency
Poaceae	60.58	51.68	Poaceae - gen.indet.p7_6	16.01	11.22	Poaceae - gen_indet.sp. p7_6	16.01	11.22
Asteraceae	8.43	14.67	*Andropogon*	10.95	6.13	Poaceae - gen_indet.sp. p2_d1	10.83	8.71
Sterculiaceae	7.83	5.69	Poaceae gen_indet.p2_d1	10.83	8.71	*Andropogon bicornis*	10.66	5.52
Lamiaceae	6.97	7.25	*Leersia*	10.52	10.79	*Leersia hexandra*	10.52	10.79
Malvaceae	4.56	5.52	*Mikania*	7.82	13.46	*Mikania congesta*	7.82	13.46

Table 4.17. Relative cover and relative frequency for family, genus and species at the PP site.

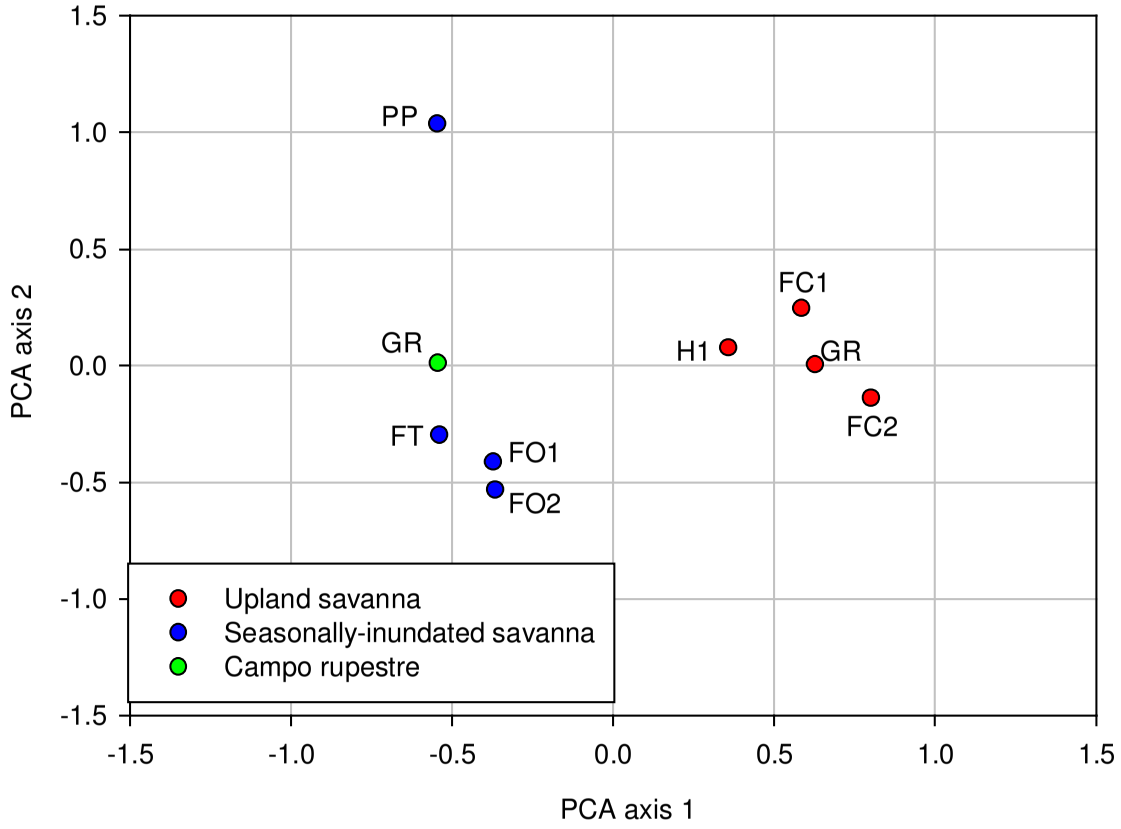

Figure 4.2. PCA site plot of relative cover of plant families at the savanna sites at NKMNP.

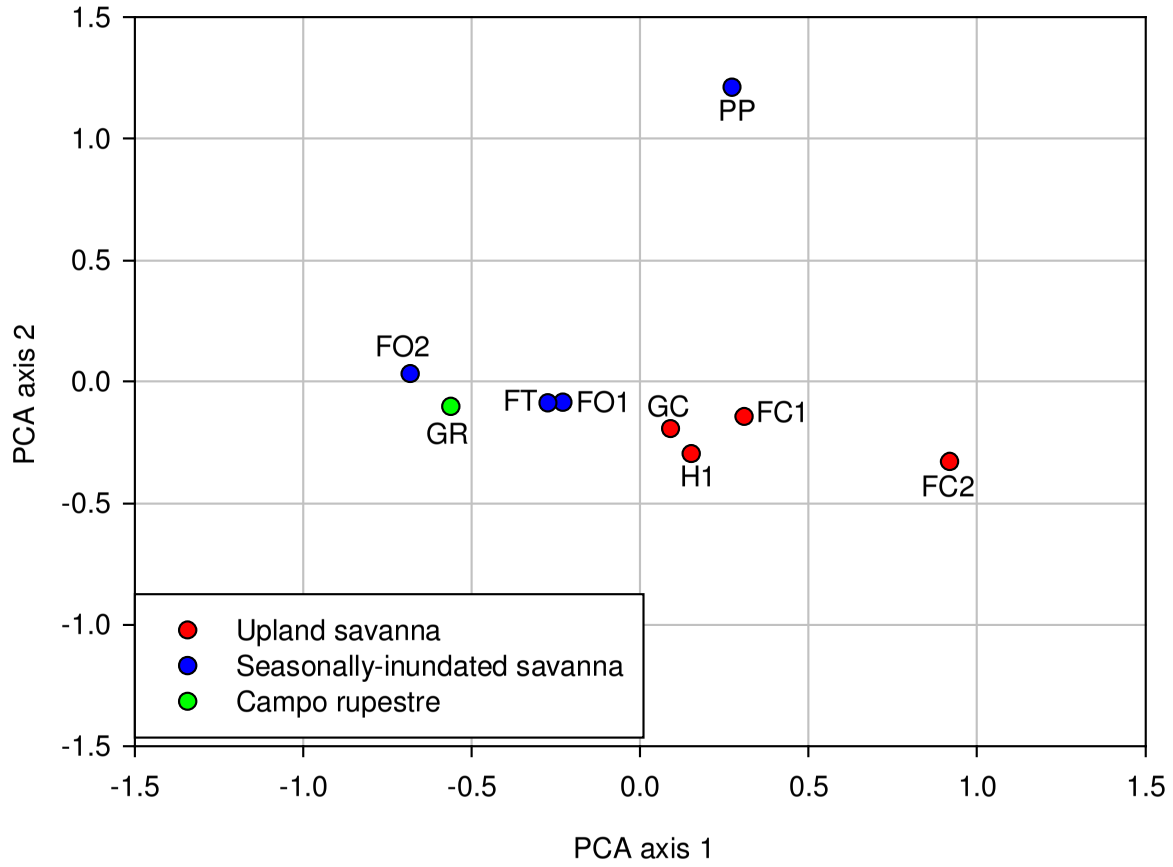

Figure 4.3. PCA site plot of relative cover of plant genera at the savanna sites at NKMNP.

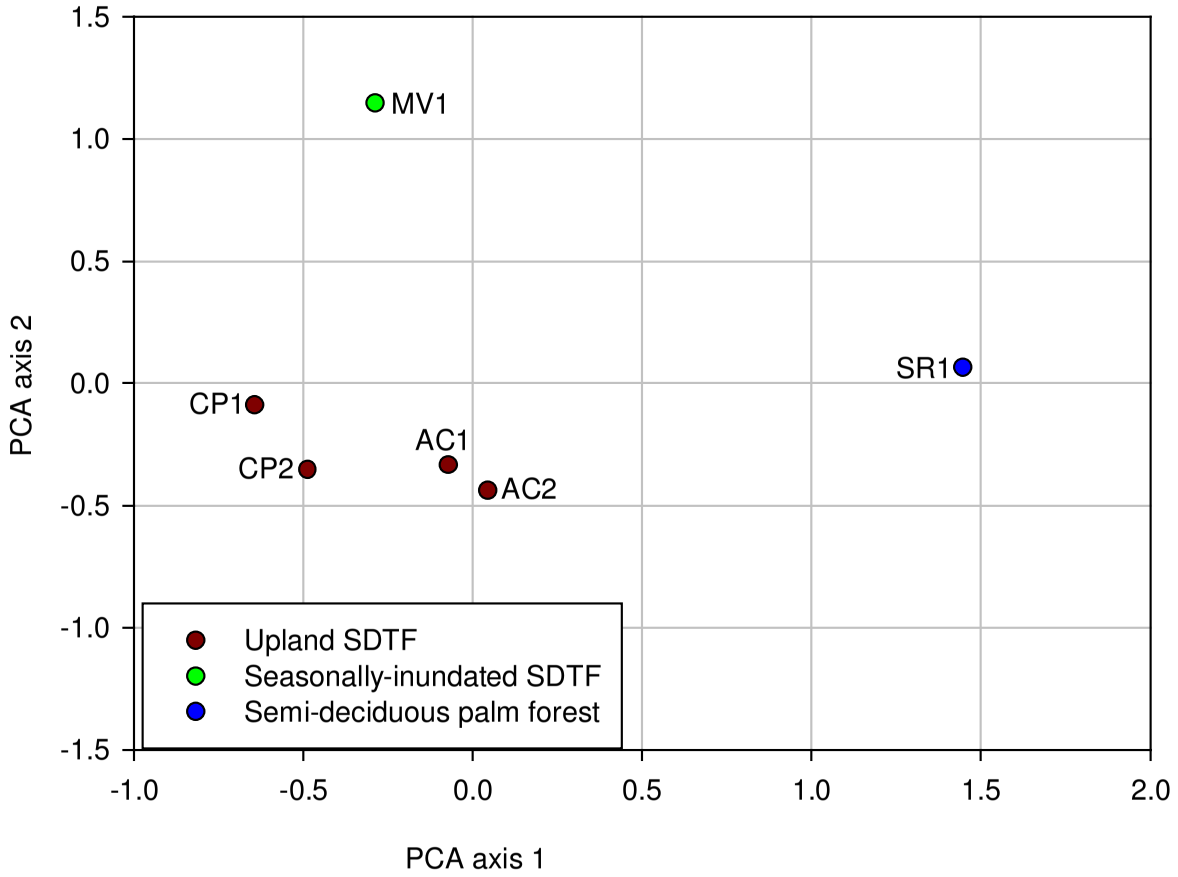

Figure 4.4. PCA site plot of % of total basal area of plant families at the SDTF sites at NKMNP.

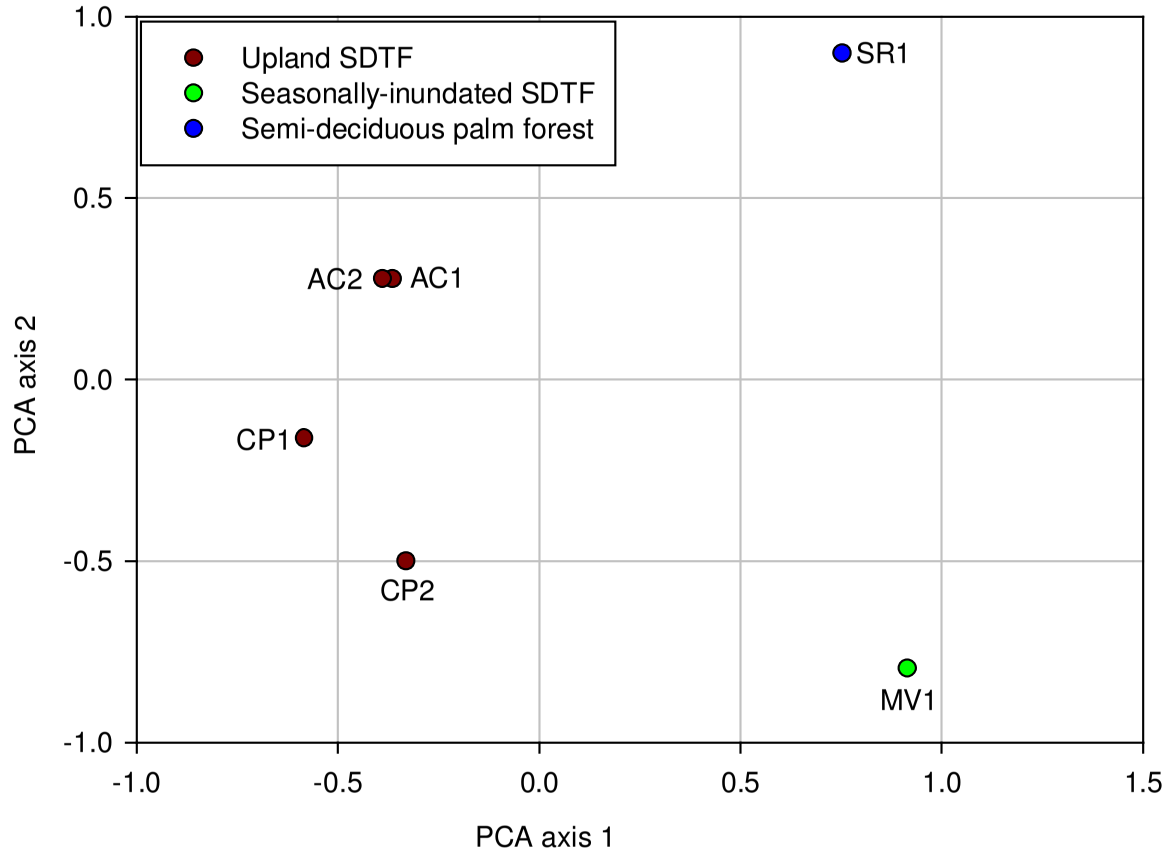

Figure 4.5. PCA site plot of % of total basal area of plant genera at the SDTF sites at NKMNP.

Taxon	Taxon score on PCA axis 1	Taxon	Taxon score on PCA axis 2
Clusiaceae	4.07	Sterculiaceae	3.26
Proteaceae	2.22	Malvaceae	3.18
Fabaceae	2.12	Asteraceae	3.09
Bombacaceae	2.11	Lamiaceae	2.89
Erythroxylaceae	2.00	Fabaceae	2.27
Lamiaceae	-1.21	Monimiaceae	-1.56
Cyperaceae	-1.35	Flacourtiaceae	-1.71
Velloziaceae	-1.45	Araliaceae	-1.85
Sterculiaceae	-1.67	Lauraceae	-1.90
Poaceae	-2.89	Cyperaceae	-1.96

Table 4.18. The key families (those with the highest magnitude taxon scores) on PCA axis 1 and PCA axis 2 for the savanna family level ordination (figure 4.2).

Taxon	Taxon score on PCA axis 1	Taxon	Taxon score on PCA axis 2
Caraipa	6.00	Poaceae - gen_indet.p7_6	7.11
Trachypogon	5.17	Poaceae - gen_indet.p2	5.85
Poaceae - gen_indet.sp11	4.91	*Leersia*	5.76
Byrsonima	2.53	*Mikania*	4.95
Ormosia	2.43	*Hyptis*	3.96
Poaceae - gen_indet.p10	-2.36	*Caraipa*	-2.80
Schizachyrium	-4.81	*Elyonurus*	-3.21
Elyonurus	-5.33	*Axonopus*	-3.64
Leptocoryphium	-5.66	*Pasapalum*	-3.75
Axonopus	-6.26	*Trachypogon*	-3.89

Table 4.19. The key genera (those with the highest magnitude taxon scores) on PCA axis 1 and PCA axis 2 for the savanna genus level ordination (figure 4.3).

Taxon	Taxon score on PCA axis 1	Taxon	Taxon score on PCA axis 2
Arecaceae	6.15	Lythraceae	3.86
Humiriaceae	0.69	Chrysobalanaceae	3.60
Dichapetalaceae	0.42	Vochysiaceae	2.46
Proteaceae	0.35	Moraceae	1.41
Araliaceae	0.13	Lauraceae	1.19
Moraceae	-1.36	Sapindaceae	-1.08
Bombacaceae	-1.56	Flacourtiaceae	-1.13
Apocynaceae	-1.59	Arecaceae	-1.29
Fabaceae	-1.82	Bombacaceae	-1.53
Combretaceae	-2.19	Sterculiaceae	-1.64

Table 4.20. The key families (those with the highest magnitude taxon scores) on PCA axis 1 and PCA axis 2 for the SDTF family level ordination (figure 4.4).

Taxon	Taxon score on PCA axis 1	Taxon	Taxon score on PCA axis 2
Orbignya	4.39	*Orbignya*	9.99
Physocalymma	3.90	*Caesalpinia*	1.76
Hirtella	3.26	*Astronium*	1.75
Qualea	2.72	*Pseudobombax*	1.69
Inga	2.27	*Dilodendron*	1.22
Spondias	-2.59	*Qualea*	-2.07
Aspidosperma	-2.65	*Spondias*	-2.63
Chorisia	-2.96	*Physocalymma*	-2.83
Combretum	-4.24	*Inga*	-2.95
Anadenanthera	-4.59	*Hirtella*	-3.23

Table 4.21. The key genera (those with the highest magnitude taxon scores) on PCA axis 1 and PCA axis 2 for the SDTF genus level ordination (figure 4.5).

4.5. Discussion

4.5.1. Savanna sites

All the savanna sites are dominated by Poaceae which has a relative cover between 42.24% (GC) and 81.46% (FO1).

For the family level ordination, axis 1 shows a good separation between the upland savanna (cerrado) sites and the seasonally-inundated savanna sites, with the cerrado sites plotting towards the positive end of the axis and the inundated sites plotting towards the negative end of the axis. The families indicative of the cerrado sites (those with positive taxon scores) are Clusiaceae, Proteaceae, Fabaceae and Bombacaceae, whilst those indicative of the seasonally-inundated sites (those with negative taxon scores) are Poaceae, Sterculiaceae and Cyperaceae.

The genus level ordination shows a similar separation, with the inundated plots concentrated towards the negative end of axis 1 and the cerrado plots having positive values on the axis 1. The taxa representative of the seasonally-inundated sites are mostly genera of grasses, such as *Axonopus, Leptocoryphium*, *Elyonurus*, *Schizachyrium* and Poaceae - gen_indet.p10. *Caraipa*, *Trachypogon,* Poaceae gen.indet sp11*, Byrsonima* and *Ormosia* all have high positive loadings on axis 1, indicative of well drained savannas.

The key taxa which are representative of upland savannas tend to be those with a woody life form e.g. *Caraipa*, *Byrsomina, Ormosia*, *Roupala* and *Bowdichia*. This reflects the visual differences between inundated and upland savannas, with the upland savannas having a well-developed woody stratum and the inundated savanna sites tending to have a poorly developed woody cover (Oliviera-Filho and Ratter, 2002). The seasonally-inundated savannas tend to have higher Poaceae cover than the upland savanna sites. The effect of inundation results in conditions unsuitable for the growth of woody vegetation, with the areas of woody vegetation in inundated savannas being restricted to areas with raised topography (e.g. termite mounds),

whereas in upland savannas the entire soil profile is well drained all year round so woody vegetation can be more extensive. Some of the woody taxa indicative of the upland savannas at NKMNP have a very widespread distribution throughout the Cerrado Biome of Brazil. For example, *Byrsonima, Roupala* and *Bowdichia* are all very abundant as shown by a study of 376 cerrado and Amazonian savanna plots across Brazil by Ratter *et al.* (2003). These three taxa are also listed as being important and widespread taxa across the savanna ecosystems of the Venezuelan Llanos (Huber *et al.,* 2006).

The most common non-graminoid genera within the seasonally flooded savannas (those with negative taxon scores on PCA axis 1) are *Ocotea, Siparuna, Curatella, Ananas* and *Didymopanax.* Some of these e.g. *Curatella* and *Didymopanax* were observed to be very common upon termite mounds within the seasonally-inundated *pampa termitero* savanna ecosystems, explaining the correspondence of some of the above taxa with the negative values on PCA axis 1. The common savanna indicator, *Curatella,* was found in this study to have a strong negative taxon score of –1.62 on the first PCA axis making it more representative of the seasonally-inundated savanna ecosystems. The likely reason for this is the common occurrence of *Curatella americana* upon the raised termite mounds within the *pampa termitero* ecosystem. Floristic surveys of a seasonally-inundated termite savanna site within Central Brazil showed that although *Curatella americana* occurred upon both the termite mounds within the inundated savanna and the surrounding upland savanna, it was found predominately within the seasonally-inundated termite savanna ecosystem, due to its ability to tolerate seasonal soil saturation (Oliveira-Filho, 1992b). Studies from Mato Grosso in Brazil have also shown that *Curatella americana* has a high tolerance of areas with a seasonally high water-table (Ratter *et al.,* 1973), such as would occur in the termite mounds within the *pampa termitero* ecosystem. This could help to explain the negative taxon score of *Curatella* and its predominance within the seasonally-inundated savannas of NKMNP.

The seasonally-inundated savanna, PP site is very distant from the rest of the savanna sites within the ordination. The reason for this is likely to be the high cover of Sterculiaceae, Malvaceae, Asteraceae and Lamiaceae at this site. It is worth noting

that the PP site experiences a greater depth of inundation than the other inundated sites under consideration (1 to 2m vs. 30 cm for the other inundated savanna sites under consideration (Panfil, 2001)) and this additional water stress is likely to be the cause of the floristic differences between the PP sites and the other inundated sites. The vegetation of this site has very few taxa with a shrub or tree life form with the majority of the taxa being of a herbaceous or graminoid life form. Although Sterculiaceae has a diverse array of life forms, the genera represented (*Melochia, Byttneria* and *Helicteres)* within the savanna plots at NKMNP all have a shrub, vine or herb life form (Killeen and Schulenberg, 1998). These taxa are also very indicative of a type of seasonally-inundated savanna ("*Pastizales de Papsalum fasciculatum")* in the extensive savanna ecosystems of the Beni Basin in northern Bolivia (Orellana *et al.,* 2004).

The *campo rupestre* site (GR) plots with the lowland seasonally-inundated sites, despite this ecosystem often being found within high altitude areas such as the tops of plateaux and mountain ridges (Oliveira-Filho and Ratter, 2002). This ecosystem develops on areas with bedrock exposure, very thin soils and with areas of marshy vegetation in areas with poor drainage. This results in there being a very limited stratum of woody plants with herbaceous cover dominating, which could explain why the GR plot is associated with the inundated plots in the ordination diagram due to the similarity of life forms in these ecosystems. The key taxon separating the *campo rupestre* site from the seasonally-inundated taxa is *Vellozia,* which is a common taxon in the *campo rupestre* sites in Brazil (Filgueiras, 2002).

4.5.2. SDTF sites

The four upland SDTF sites contain species typical of the Chiquitano dry forest region of lowland Bolivia. *Combretum leprosum* is a common species within the CP1, CP2, AC1 and AC2 sites and is a common species on well-drained soils within the Chiquitano dry forest (Jardim *et al.,* 2003). *Combretum* is also an important genus of dry forests across the Neotropics (Marchant *et al.,* 2002), suggesting that this taxon is common in dry forests over a wide geographical area. *Tabebuia* species are also common within the upland SDTF sites, e.g. *T.roseo-alba* and *T.*

impetiginosa are common and both these species are common deciduous trees within the Chiquitano dry forest (Jardim *et al.,* 2003). Another key taxon of the upland SDTF sites is *Anadenanthera colubrina* which is recognised as a key characteristic species of the Chiquitano dry forest (Killeen, 1998). *Anadenanthera colubrina* and *Combretum leptosum* have been used as indicator taxa for the phytogeographic unit of seasonally dry forests in South America (Prado, 2000), indicating the widespread geographical distribution of these two taxa. *Casearia* spp. are mostly subcanopy trees and have wide ecological and geographical ranges across the Neotropics but is also common taxon within the Chiquitano dry forest (Gentry, 1993; Jardim *et al.,* 2003). *Simira* spp. are mid-canopy to canopy trees and are especially common in dry forest (Gentry, 1993) and there is a species *(Simira rubescens)* which is common within the Chiquitano dry forest (Jardim *et al.,* 2003). *Aspidosperma* is a genus of large trees with 80 species (Gentry, 1993) and has many species that are common within dry forest communities, for example, four species are found within the Chiquitano dry forest (Jardim *et al.,* 2003). Two *Aspidosperma* species (*A cylindocarpon* and *A. macrocarpon*) are common in the upland SDTF of NKMNP. Hence these four upland SDTF sites appear to contain taxa representative of the Chiquitano dry forest complex of Bolivia and also seasonal dry forests across the Neotropics (e.g. *Combretum leprosum* and *Anadenanthera colubrina*).

The dominant taxon at the seasonally-inundated semi-deciduous forest site (MV1) is *Physocalymma scaberrimum* and is identified by Killeen *et al.* (2006), as being important within the North-Central region of the Chiquitano dry forest and is also common at the ecotone between SDTF and Cerrado (Jardim *et al.,* 2003). The other dominant taxa are more indicative of evergreen forest sites (e.g. *Hirtella gracilipes, Inga ingoides* and *Sorocea guilleminiana*).

The taxa which have high weighting towards the negative end of axis 1 are taxa that are well represented within the Chiquitano dry forest area of Bolivia on well-drained soils as discussed above. The taxa with high weightings on the positive side of axis one are taxa that are likely to prefer wetter (mesic and inundated) environments. The taxa representative of the MV1 plot include some which are more representative of evergreen forest sites e.g. *Hirtella, Inga* and *Sorocea* (Killeen and Schulenberg,

1998), which are generally absent or in much lower abundance at the other five upland SDTF plots. These species can probably thrive at this site despite it being surrounded by more deciduous vegetation because the poorly drained soils provide a source of moisture for most of the year. The second PCA axis at the genus level separates the inundated SDTF plot (MV1) from the semi-deciduous palm forest site (SR1). The key genera indicative of the SR1 plot are *Orbignya* (*Attalea), Astronium* and *Pseudobombax. Attalea speciosa* is a key taxon indicative of this forest type and is often found within riverine forests and marshy places (Jardim *et al.,* 2003). Surprisingly this taxa is absent from the inundated SDTF site (MV1), which has greater water availability than the SR1 site.

4.6. Conclusions

The importance of this research is to indicate that different families and genera within seasonally dry tropical forests and savannas ecosystems of Noel Kempff Mercado National Park, Bolivia have different ecological preferences. The results test the floristic differences between different forest and savanna ecosystems in NE Bolivia, using inundation regime as the key environmental variable. The findings show that areas of SDTF within seasonally-inundated settings are floristically distinct from SDTF found in upland, *terra firme,* areas, with the presence of *Hirtella, Inga, Physocalymma* and *Sorocea* being indicative of the seasonally-inundated SDTF. *Combretum, Anadenanthera, Casaeria, Simira* and *Aspidosperma* are indicative of upland SDTF ecosystems. The semi-deciduous palm forest is dominated by the presence of *Orbignya (Attalea) speciosa.* For the savanna plots, a good floristic separation of seasonally-inundated savannas and upland *terra firme* savannas is described. Although both types are dominated by Poaceae, the families Sterculiaceae, Cyperaceae and Lamiaceae are inferred to be indicative of the seasonally-inundated savannas and the families Clusiaceae, Proteaceae, Bombaceae, Fabaceae and Erythoxylaceae indicative of the upland savannas. Velloziaceae is representative of *campo rupestre.*

The findings listed above will be important for inferring the ecological preferences of the taxa listed within this study, as many of them have a widespread distribution across savanna and seasonally dry tropical forest ecosystems of the Neotropics (Marchant *et al.,* 2002). Although the floristic composition of savanna and SDTF sites is often heterogeneous due to the different edaphic (e.g. water and nutrient availability) and climatic conditions (e.g. Ratter *et al.,* 2003; Huber *et al.,* 2006), the edaphic environment and water-availability are key factors influencing the vegetation of ecosystems across the Neotropics.

4.7. Summary of chapter

The results of this chapter show that the seasonally-inundated and upland savannas and seasonally dry tropical forests are well differentiated by their floristic inventories at the family and genus level. This means that it is possible that these ecosystems may be differentiated by their modern pollen rain as this will be a function of the floristic inventories of the ecosystems. That the separation is evident at a relatively crude taxonomic level (family and genus) is important as neotropical pollen grains can seldom be identified to species level. The next two chapters will investigate the feasibility of characterising and differentiating these ecosystems by their modern pollen rain.

Chapter 5. Characterisation of neotropical savannas and seasonally dry tropical forests by their modern pollen rain

Contents

5.1. Introduction to chapter *90*

5.2. Methodology *90*

5.3. Statistical analysis *98*

5.4. Descriptions of the vegetation of the sampling sites *100*

5.4.1. Toledo - Seasonally-inundated savanna (TO1) 100

5.4.2. Monte Verde - Seasonally-inundated SDTF (MV1) 101

5.4.3. Cerro Pelao - Upland SDTF (CP1) 101

5.4.4. Los Fierros – Upland savanna (FC1) 101

5.4.5. Los Fierros – Seasonally-inundated savanna (FT) 101

5.4.6. Description of vegetation surrounding the Beni lakes 102

5.4.7. Description of vegetation surrounding the Pantanal lakes 102

5.5. Results *109*

5.5.1. TO1 - Seasonally-inundated savanna 109

5.5.2. FC1 – Upland savanna 109

5.5.3. FT – Seasonally-inundated savanna 109

5.5.4. MV1 - Seasonally-inundated SDTF 109

5.5.5. CP1 - Upland SDTF 110

5.5.6. Beni Basin lake sediment results 110

5.5.7. SDTF lake sediment results 111

5.5.8. Pollen accumulation rates 111

5.5.9. Pollen/vegetation relationships 112

5.5.10. Moraceae/Urticaceae differentiation of NKMNP pollen traps 112

5.5.11. Comparison between pollen signals from artificial pollen traps and surface lake sediments 112

5.6. Discussion *133*

5.6.1. Modern pollen rain from savanna ecosystems 133

5.6.2. Modern pollen rain of SDTF ecosystems 139

5.6.3. Pollen/vegetation relationships 144

5.6.4. Pollen accumulation rates 148

5.6.5. Inter-annual variability 148

5.6.6. Intra-site variability 149

5.6.7. Comparison between pollen signals from artificial pollen traps and surface lake sediments 151

5.7. Summary of chapter *153*

5.1. Introduction to chapter

The aim of this chapter is to characterise the modern pollen rain of savanna and seasonally dry tropical forest (SDTF) ecosystems in areas of the southern Neotropics. The modern pollen rain was sampled using both artificial pollen traps and surface lake sediments. The key pollen taxa found in each ecosystem are described and the results are then compared with vegetation inventories. This allows pollen-vegetation relationships to be calculated so taxa that are over-represented, under-represented or absent in the modern pollen rain can be identified. Multiple pollen traps were sampled from the study sites allowing the intra-site and inter-annual variability in the modern pollen rain to be investigated. The results from this research are then compared with other pollen rain studies from the region and the implications for the interpretation of fossil pollen records are considered.

5.2. Methodology

The modern pollen rain of various physiognomies of savanna and SDTF was sampled from within several different geographic regions of Bolivia (figure 5.1). Detailed figures of sites within the Beni Basin, the Pantanal and Noel Kempff Mercado National Park are illustrated in figures 5.2, to 5.5. These sites are described in chapter 2 and the sampling, sample preparation and pollen counting methodology is described in chapter 3.

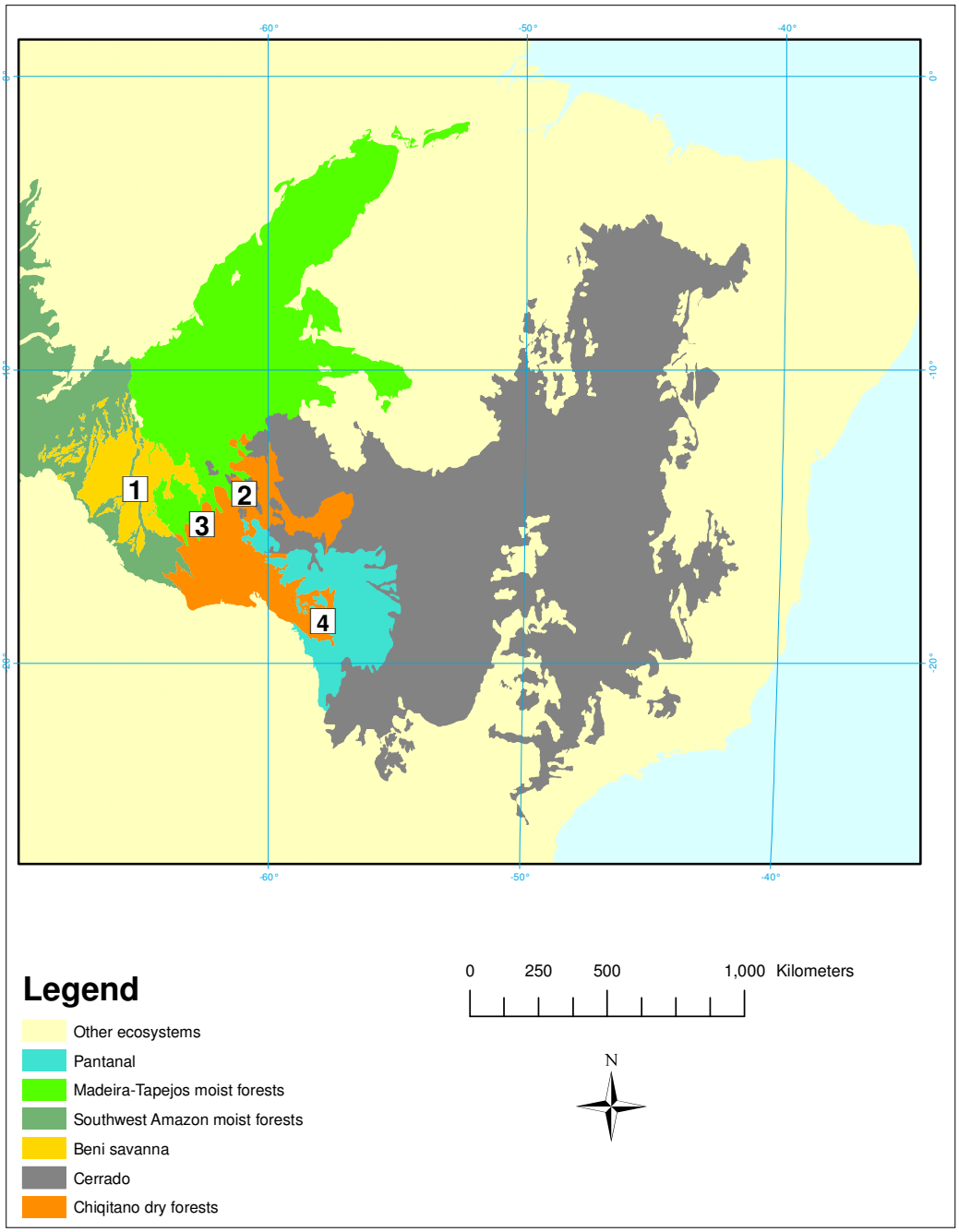

Figure 5.1. Locations and ecology of the study sites for this research. 1. The Beni Basin. 2. Noel Kempff Mercado National Park. 3. Laguna Socorros (Beni). 4. Laguna La Gaiba and Laguna Mandioré (The Pantanal). Ecoregions from from Olson *et al.* (2001). Base data from http://geodata.grid.unep.ch.

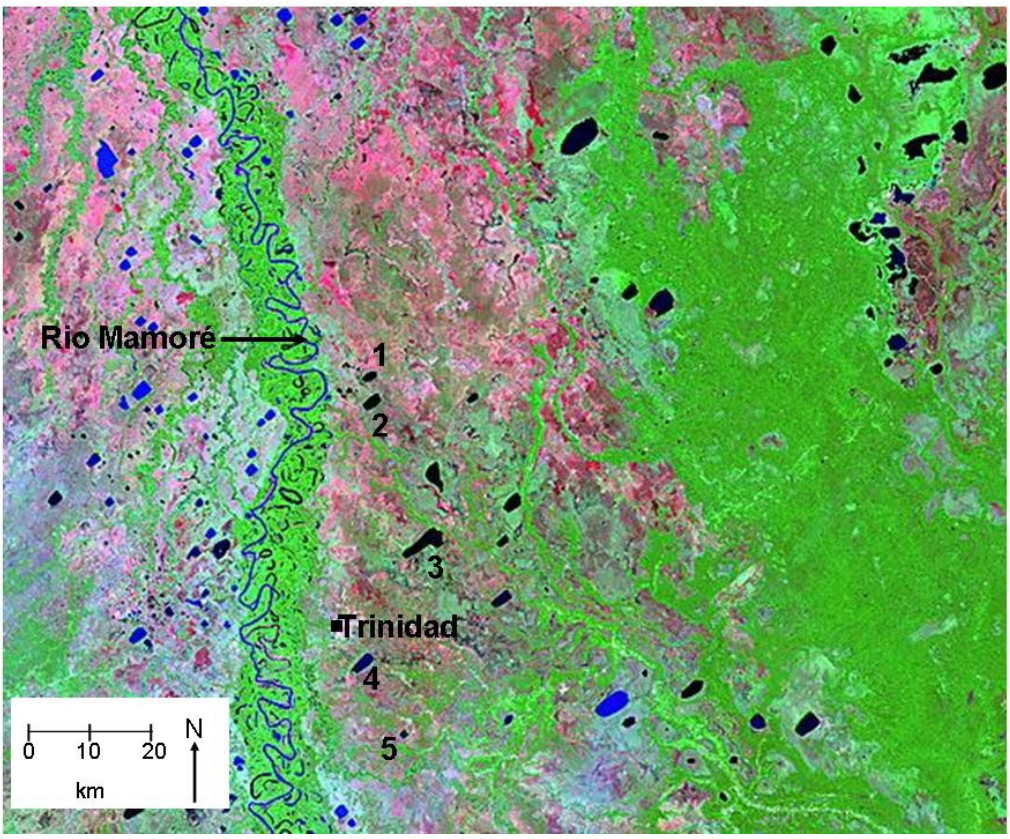

Figure 5.2. Figure showing the ecosystems surrounding the lakes sampled for their modern pollen rain from the Beni Basin. Forest areas are represented by the green colour, whilst other colours represent open savanna ecosystems. 1 = Laguna Belen, 2 = Laguna Coitarama, 3 = Laguna Cernandez, 4 = Laguna Suarez, 5 = Laguna Azul. Also marked on the map are the Rio Mamoré and the city of Trinidad. Image modified from University of Maryland Global Land Cover Facility, http://glcf.umiacs.umd.edu/data.

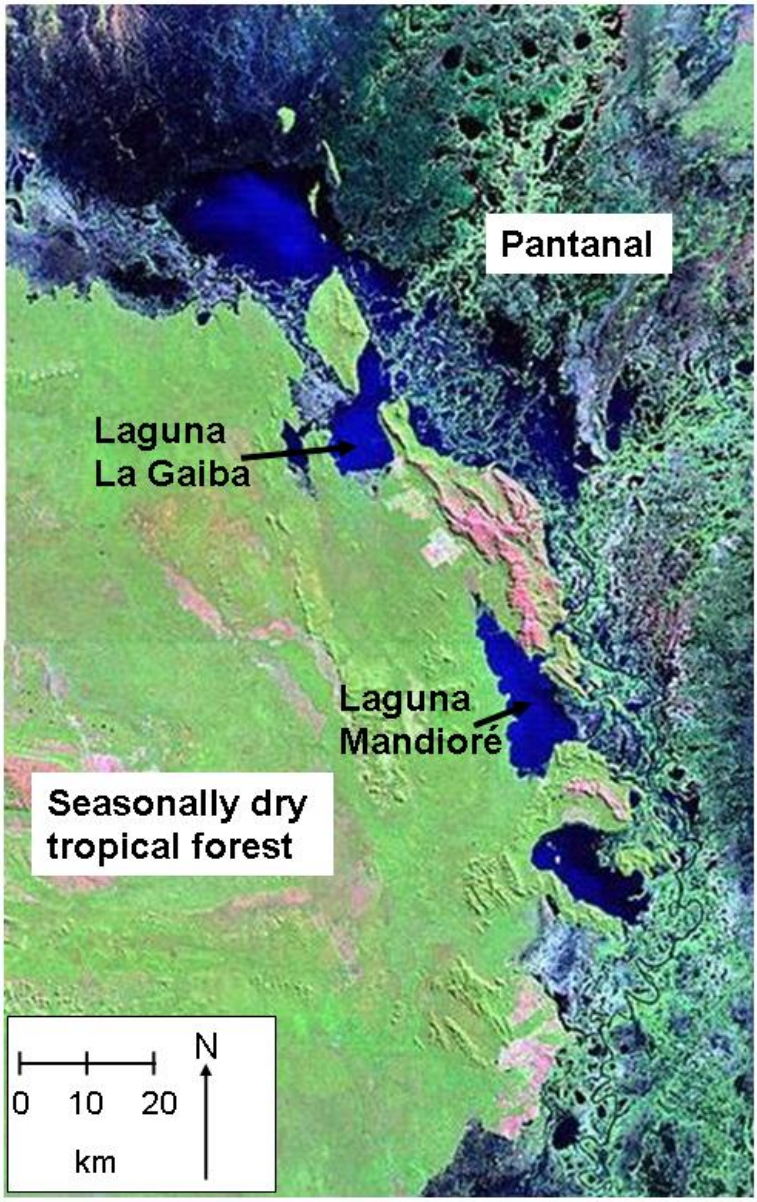

Figure 5.3. Figure showing the ecosystems surrounding the two lakes sampled from the Bolivian Pantanal. Image modified from University of Maryland Global Land Cover Facility, http://glcf.umiacs.umd.edu/data.

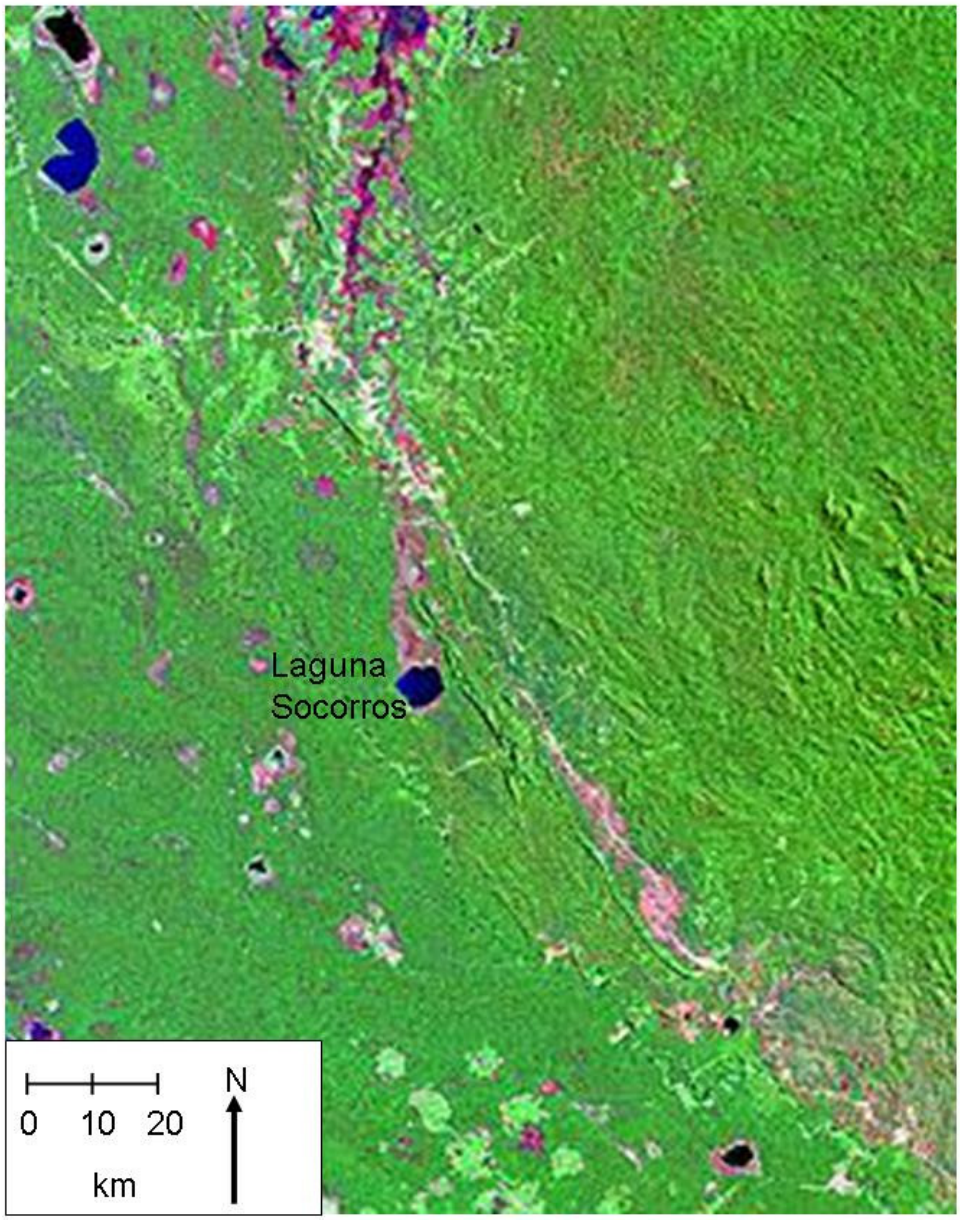

Figure 5.4. Figure showing the ecosystems surrounding Laguna Socorros. The green colours represent SDTF, whiles red areas represent open vegetation. Image modified from University of Maryland Global Land Cover Facility, http://glcf.umiacs.umd.edu/data

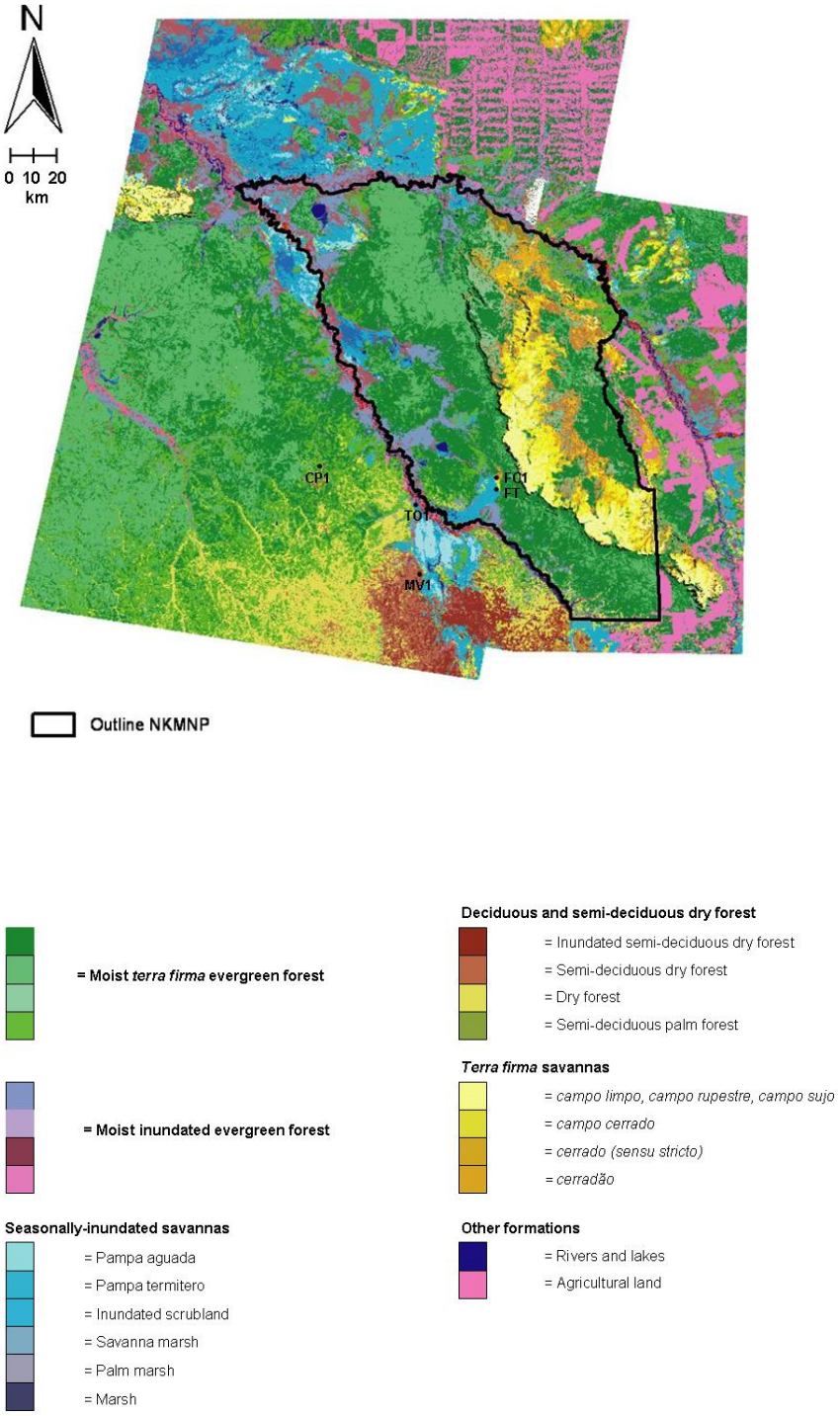

Figure 5.5. Location of study sites within NKMNP, Bolivia. (modified from Killeen *et al.,* 1998).

Plot	Sampling strategy	Latitude (S)	Longitude (W)	Site name	Ecosystem	Substrate	Slope (degrees)	Inundation regime	Altitude (m)
FC1	Artificial pollen traps	14°36'25"	60°51'23"	Los Fierros	Cerrado savanna	Tertiary laterite	0	None	200
FT	Artificial pollen traps	14°36'53"	60°51'59"	Los Fierros	Termite savanna	Quaternary sediments	0	Seasonal	200
CP1	Artificial pollen traps	14°32'28"	61°29'53"	Cerro Pelao	Deciduous forest	Granitic	20	Xeric	400
TO1	Artificial pollen traps	14°43'41"	61°08'16"	Toledo	Termite savanna	Quaternary sediments	0	Seasonal	~200
MV1	Artificial pollen traps	14°56'27"	61°07'59"	Monte Verde	Seasonally-inundated semi-deciduous forest	Quaternary sediments	0	Seasonal	230

Table 5.1. Sampling sites of artificial pollen traps in Noel Kempff Mercado National Park.

Lake	Sampling strategy	Latitude (S)	Longitude (W)	Ecosystem
Laguna Azul	Surface lake sediments	14°59'27"	64°48'45"	Seasonally-inundated savanna
Laguna Belen	Surface lake sediments	14°27'18"	64°51'30"	Seasonally-inundated savanna
Laguna Suarez	Surface lake sediments	14°52'51"	64°51'59"	Seasonally-inundated savanna
Laguna Cernandez	Surface lake sediments	14°41'18"	64°45'55"	Seasonally-inundated savanna
Laguna Coitarama	Surface lake sediments	14°30'10"	54°51'39"	Seasonally-inundated savanna
Laguna Socorros	Surface lake sediments	16°08'	63°07'	Seasonally dry tropical forest
Laguna Mandioré	Surface lake sediments	18°05'	57°33'	Seasonally-inundated savanna / Seasonally dry tropical forest
Laguna La Gaiba	Surface lake sediments	17°47'	57°43'	Seasonally-inundated savanna / Seasonally dry tropical forest

Table 5.2. Sampling sites for surface lake sediment.

5.3. Statistical analysis

The traps were collecting pollen for the duration of one year, therefore pollen accumulation rates for the artificial pollen traps were calculated using equation 5.1.

$$\text{Influx of pollen into the trap (grains year}^{-1}\text{)} = \frac{\text{modern pollen counted x exotic pollen added}}{\text{exotic pollen counted}}$$

$$\text{Pollen accumulation rate (grains cm}^{-2}\text{ year}^{-1}\text{)} = \frac{\text{influx of pollen into the trap}}{\text{surface area of the trap}}$$

Equation 5.1. Formulae to calculate pollen accumulation rates for artificial pollen traps (after Birks and Birks, 1980; Gosling, 2004).

Pollen concentration data for the surface lake sediments were calculated using equation 5.2.

$$\text{Pollen concentration (grains cm}^{-3}\text{)} = \frac{\text{Modern pollen counted x exotic pollen added}}{\text{exotic pollen counted}}$$

Equation 5.2. Formula to calculate pollen concentration for surface lake sediments (after Birks and Birks, 1980).

Pollen/vegetation (p/v) ratios were calculated for the pollen trap data from NKMNP (*as per* Gosling *et al.,* in press) to investigate which taxa in the vegetation plots were over/under-represented in the pollen rain. As different methods were used to sample the vegetation in the savanna ecosystems compared to the forest ecosystems, two different formulae were used to calculate the p/v ratios. For the savanna plots equation 5.3 was used.

$$\text{Pollen/vegetation ratio} = \frac{\text{pollen taxon abundance (\%)}}{\text{relative cover of taxon in the vegetation plot (\%)}}$$

Equation 5.3. Formula to calculate pollen/vegetation ratios for savanna data.

For the forest data equation 5.4 was used.

$$\text{Pollen/vegetation ratio} = \frac{\text{pollen taxon abundance (\%)}}{\text{\% number of stems in the vegetation plot}}$$

Equation 5.4. Formula to calculate pollen/vegetation ratios for forest data.

It must be appreciated that because only plants with a diameter at breast height (dbh) ≥10 cm were sampled in the forest plots, pollen/vegetation ratios cannot be calculated for herbs/shrubs/small trees within the plot with a dbh < 10 cm due to the lack of quantitative data about the abundances of these taxa. As stressed by Gosling *et al.* (in press), the p/v ratios are not intended to be a statistically robust numeric to allow relative vegetation cover to be reconstructed from fossil pollen records (*as per* Davis, 1963). This is because of inherent assumptions in the method, such as the problem of pollen source area, as it is very difficult to separate pollen produced by plants within the vegetation plot from that of vegetation outside the plot. They are only presented as an index for investigating relative pollen production from plants within the study sites.

Cluster analysis was used to investigate the similarity between the modern pollen spectra obtained from the surface lake sediments and the artificial pollen traps on the basis of their taxonomic composition. The intention was to test whether samples from the SDTF ecosystems are similar to each other regardless of sampling strategy (artificial pollen traps and surface lake sediments) and to test the same criterion for the samples from the seasonally-inundated savannas. The average modern pollen rain signal from each lake and the average annual modern pollen rain from the artificial pollen trap sites were calculated and this data was used in the analysis. The data were square-root transformed to reduce the influence of major taxa (Birks, 1986; Prentice, 1986) and a distance matrix for the samples was calculated using squared Euclidean distance as the numeric. The average-linkage clustering method, which is the most widely used agglomerative clustering method in ecology (van Tongeren, 1995) was used to plot the cluster dendrogram. The analysis was performed using R (R Development Core Team, 2007).

For the artificial pollen trap data, the results presented in this chapter are mean pollen percentages calculated from the twelve pollen traps analysed from each site. For the lake sediment data, the results presented are mean values from a number of surface samples taken from each lake. The number of different samples collected from each lake is given in sections 5.5.6 and 5.5.7. The justification for presenting the mean rather than the median is that the median would ignore any pollen taxa that had sporadically high percentage values in certain pollen traps or lake surface samples. For example, if a pollen taxon were represented in less than half of the pollen traps/surface lake sediments from a site, the median would be zero, which would give an unrepresentative impression of its representation in the modern pollen rain.

5.4. Descriptions of the vegetation of the sampling sites

Detailed vegetation inventories of all plants with a dbh ≥ 10 cm from within a 500 m by 20 m plot MV1 and CP1 plots, and line transect surveys of plants within the savanna sites FC1 and FT, are available through the SALVIAS database (SALVIAS, 2008). Detailed discussion of the vegetation sampling strategy can be found in section 3.2.3.

5.4.1. Toledo - Seasonally-inundated savanna (TO1)

This site is covered by a type of seasonally-inundated savanna called *pampa termitero,* which consists of a vast grassy plain with scattered islands of trees and shrubs growing upon raised mounds often colonised by termites (see chapter 2 for a detailed discussion of the physiognomy of this ecosystem). No quantitative vegetation data are available from this site. However, observations were made upon the key vegetation types during August 2006. The vast grassy plain was dominated by gramineous vegetation with scattered herbs of *Borreria* spp. (Rubiacaeae)*, Hyptis* spp. (Lamiaceae) and Melastomataceae. Upon the termite mounds, various types of woody vegetation were present e.g. *Dipteryx alata* (Fabaceae)*, Curatella americana* (Dilleniaceae)*, Tabebuia* sp. (Bignoniaceae)*, Vochysia* sp. (Vochysiaceae), along

with the palms *Mauritia* sp. and *Mauritiella* sp. The termite mounds tended to have a diameter between 2 and 5 meters.

5.4.2. Monte Verde - Seasonally-inundated SDTF (MV1)

This site is found within the valley bottom and is inundated during the wet season. The top five species (see table 5.3) within this site are *Physocalymma scaberrimum* (Lythraceae), *Hirtella gracilipes* (Chrysobalanaceae), *Inga ingoides* (Fabaceae), *Sorocea guilleminiana* (Moraceae) and *Xylopia sericea* (Annonaceae).

5.4.3. Cerro Pelao - Upland SDTF (CP1)

This site is situated upon a granitic inselberg and is surrounded by evergreen forest. The top five species (see table 5.4) within this plot are *Combretum leprosum* (Combretaceae), *Aspidosperma cylindrocarpon* (Apocynaceae), *Anadenanthera colubrina* (Fabaceae), *Luehea candicans* (Tiliaceae) and *Spondias mombin* (Anacardiaceae).

5.4.4. Los Fierros – Upland savanna (FC1)

This site is covered by a type of upland savanna called *campo cerrado* which consists of grassland with scattered trees and shrubs. The dominant family in terms of relative cover is Poaceae (51.01%). The key species in the plot are presented in table 5.5. The most common woody species (trees and shrubs) within the site in terms of numbers of stems are *Eugenia parvifolia* (Myrtaceae), 53 stems; *Davilla grandifolia* (Dilleniaceae), 29 stems; *Zamia boliviana (*Cycadaceae), 20 stems; *Roupala montana* (Proteaceae), 16 stems; and *Ouratea spectabilis* (Ochnaceae), 14 stems.

5.4.5. Los Fierros – Seasonally-inundated savanna (FT)

This site is the same type of seasonally-inundated savanna as the Toledo site, however, the diameter of the termite mounds was smaller than those observed at the TO1 site, only reaching 1-2m in diameter. This resulted in the trees and shrubs colonising these termite mounds being of a much smaller size than those observed at TO1 site. The key species in the plot are presented in table 5.6. The ground cover is

dominated by Poaceae (Relative cover = 74.93%) and Cyperaceae (Relative cover = 7.13%). The most common woody species (trees and shrubs) within the site in terms of number of stems are *Melochia spicata* (Sterculiaceae), 22 stems; *Casearia arborea* (Flacourtiaceae), 9 stems; *Ayapana amygdalina* (Asteraceae), 8 stems; *Hyptis velutina* (Lamiaceae), 6 stems; and *Annona excellens* (Annonaceae), 6 stems.

5.4.6. Description of vegetation surrounding the Beni lakes

Five lakes (Laguna Azul, Laguna Belen, Laguna Cernandez, Laguna Coitarama and Laguna Suarez) were sampled from within seasonally-inundated savanna ecosystems of the Beni Basin within the Beni *departamento* of Bolivia (table 5.2). These lakes were generally all shallow and flat-bottomed, with the maximum depth of any of the lakes sampled being just 2 m during the dry season. They were largely surrounded by open vegetation formations but had patches of forest islands and areas of gallery forest scattered around their margins (figure 5.2). Another lake (Laguna Socorros) was sampled from within the SDTF ecosystems from the extreme south of the Beni *departamento* (table 5.2, figure 5.3)

5.4.7. Description of vegetation surrounding the Pantanal lakes

Two lakes (Laguna La Gaiba and Laguna Mandioré) were sampled from the western margins of the Pantanal (table 5.2). These lakes are bordered on their western margin by the Chiquitano dry forest and to the east by the seasonally inundated savannas and permanent marshes of the Pantanal complex (figure 5.3). Both lakes had extensive areas of aquatic vegetation around their margins, the dominant taxa were observed to be Poaceae and *Eichhornia* spp.

Family	Genus	Species	Number of stems	% number of stems	Total basal area (cm^2)	% of total basal area
Lythraceae	*Physocalymma*	*scaberrimum*	117	13.43	43221.00	19.47
Chrysobalanaceae	*Hirtella*	*gracilipes*	114	13.09	34562.18	15.57
Fabaceae	*Inga*	*ingoides*	63	7.23	11150.78	5.02
Moraceae	*Sorocea*	*guilleminiana*	38	4.36	701.70	0.32
Annonaceae	***Xylopia***	***sericea***	**29**	**3.33**	**2820.77**	**1.27**
Fabaceae	*Inga*	*laurina*	28	3.21	11686.28	5.26
Fabaceae	***Bauhinia***	***rufa***	**20**	**2.30**	**3943.82**	**1.78**
Vochysiaceae	***Qualea***	***cordata***	**20**	**2.30**	**19602.08**	**8.83**
Moraceae	*Cecropia*	*concolor*	19	2.18	3685.76	1.66
Anacardiaceae	***Tapirira***	***guianensis***	**15**	**1.72**	**938.59**	**0.42**
Bignoniaceae	*Tabebuia*	*serratifolia*	14	1.61	3410.19	1.54
Lauraceae	***Nectandra***	***acutifolia***	**14**	**1.61**	**2981.74**	**1.34**
Euphorbiaceae	*Pera*	*barbinervis*	13	1.49	4759.38	2.14
Lacistemataceae	***Lacistema***	***aggregatum***	**12**	**1.38**	**154.67**	**0.07**
Lecythidaceae	***Cariniana***	***domestica***	**12**	**1.38**	**2300.44**	**1.04**
Sapindaceae	*Cupania*	*cinerea*	12	1.38	595.80	0.27
Moraceae	*Brosimum*	*lactescens*	11	1.26	4105.20	1.85
Bombacaceae	***Ceiba***	***samauma***	**9**	**1.03**	**7345.04**	**3.31**
Combretaceae	*Terminalia*	*amazonia*	9	1.03	7730.11	3.48
Fabaceae	*Bowdichia*	*virgilioides*	9	1.03	1891.25	0.85
Fabaceae	*Dalbergia*	*gracilis*	9	1.03	1656.60	0.75
Myrtaceae	*Eugenia*	*florida*	9	1.03	324.74	0.15
Rubiaceae	*Uncaria*	*guianensis*	9	1.03	342.65	0.15

Table 5.3. Species in the MV1 plot with a percentage of total stems (with a dbh ≥10 cm) greater than 1%. The taxa in bold are those which are absent from the modern pollen rain of the site.

Family	Genus	Species	Number of stems	% number of stems	Total basal area (cm^2)	% of total basal area
Combretaceae	*Combretum*	*leprosum*	107	16.98	26906.53	13.11
Apocynaceae	***Aspidosperma***	***cylindrocarpon***	**57**	**9.05**	**19511.19**	**9.51**
Fabaceae	*Anadenanthera*	*colubrina*	50	7.94	29061.30	14.16
Tiliaceae	*Luehea*	*candicans*	48	7.62	7475.91	3.64
Anacardiaceae	***Spondias***	***mombin***	**39**	**6.19**	**20247.16**	**9.86**
Apocynaceae	***Aspidosperma***	***macrocarpon***	**35**	**5.56**	**11774.69**	**5.74**
Bignoniaceae	*Tabebuia*	*impetiginosa*	28	4.44	10177.19	4.96
Vochysiaceae	***Callisthene***	***fasciculata***	**25**	**3.97**	**10348.41**	**5.04**
Euphorbiaceae	*Sebastiania*	*huallagensis*	20	3.17	2658.49	1.30
Fabaceae	***Bauhinia***	***rufa***	**19**	**3.02**	**2157.98**	**1.05**
Flacourtiaceae	*Casearia*	*gossypiosperma*	17	2.70	3628.54	1.77
Fabaceae	***Amburana***	***cearensis***	**16**	**2.54**	**6245.20**	**3.04**
Anacardiaceae	*Astronium*	*urundeuva*	12	1.90	3592.73	1.75
Fabaceae	***Platymiscium***	***sp.1***	**12**	**1.90**	**3012.64**	**1.47**
Bombacaceae	***Pseudobombax***	***longiflorum***	**10**	**1.59**	**9293.62**	**4.53**
Rhamnaceae	*Rhamnidium*	*elaeocarpum*	10	1.59	2505.62	1.22
Fabaceae	*Acacia*	*polyphylla*	8	1.27	961.72	0.47
Sapindaceae	*Talisia*	*esculenta*	8	1.27	1083.26	0.53
Sapotaceae	*gen_indet.*	*sp.1*	8	1.27	1259.34	0.61
Annonaceae	***Duguetia***	***furfuracea***	**7**	**1.11**	**538.59**	**0.26**
Fabaceae	*Dipteryx*	*alata*	7	1.11	3685.09	1.80

Table 5.4. Species in the CP1 plot with a % of total stems (with a dbh ≥10 cm) greater than 1%. The taxa in bold are those which are absent from the modern pollen rain of the site.

Family	Genus	Species	Total cover (cm)	Number of occurrences	Relative cover (%)	% Number of occurrences
Poaceae	*Andropogon*	*virgatus*	1526	264	12.43	17.83
Poaceae	*Paspalum*	*pectinatum*	1297	169	10.57	11.41
Poaceae	*Elyonurus*	*muticus*	1270	96	10.35	6.48
Poaceae	*Paspalum*	*stellatum*	1206	309	9.82	20.86
Rubiaceae	*Borreria*	*sp.1*	599	47	4.88	3.17
Dilleniaceae	*Davilla*	*grandiflora*	465	29	3.79	1.96
Poaceae	*Trachypogon*	*plumosus*	412	84	3.36	5.67
Celastraceae	***Maytenus***	***spinosa***	**400**	**3**	**3.26**	**0.20**
Lythraceae	***Lafoensia***	***vandelliana***	**315**	**9**	**2.57**	**0.61**
Bombacaceae	***Eriotheca***	***gracilipes***	**300**	**1**	**2.44**	**0.07**
Myrtaceae	*Eugenia*	*parviflora*	292	53	2.38	3.58
Fabaceae	***Bauhinia***	***rufa***	**235**	**11**	**1.91**	**0.74**
Proteaceae	*Roupala*	*montana*	233	16	1.90	1.08
Malpighiaceae	*Byrsonima*	*fagifolia*	214	9	1.74	0.61
Bignoniaceae	***Tabebuia***	***roseo-alba***	**200**	**1**	**1.63**	**0.07**
Poaceae	*Axonopus*	*pulcher*	176	23	1.43	1.55
Caryocaraceae	***Caryocar***	***brasiliense***	**165**	**4**	**1.34**	**0.27**
Fabaceae	*Ormosia*	*sp.1*	150	1	1.22	0.07
Ochnaceae	***Ouratea***	***spectabilis***	**142**	**14**	**1.16**	**0.95**
Clusiaceae	***Caraipa***	***densifolia***	**126**	**12**	**1.03**	**0.81**
Myrtaceae	*Myrcia*	*regnelliana*	125	3	1.02	0.20
Poaceae	*Paspalum*	*pumilum*	123	25	1.00	1.69
Moraceae	*Brosimum*	*gaudichaudii*	114	11	0.93	0.74
Flacourtiaceae	***Casearia***	***sylvestris***	**102**	**5**	**0.83**	**0.34**

Table 5.5 Continued overleaf.

Malpighiaceae	*Tetrapteris*	*ambigua*	101	8	0.82	0.54
Fabaceae	***Diptychandra***	***aurantiaca***	**90**	**1**	**0.73**	**0.07**
fam_indet.	*gen_indet.*	*sp.6*	90	1	0.73	0.07
Poaceae	*Paspalum*	*geminiflorum*	88	14	0.72	0.95
Myrtaceae	*Myrcia*	*subsessilis*	82	2	0.67	0.14
Ochnaceae	***Ouratea***	***sp.3***	**80**	**3**	**0.65**	**0.20**
Sapotaceae	*Pouteria*	*ephedrantha*	77	3	0.63	0.20

Table 5.5. Species in the FC1 plot with a % of total cover greater than 0.5%. The taxa in bold are those which are absent from the modern pollen rain of the site.

Family	Genus	Species	Total cover (cm)	Number of occurrences	% cover	% number of occurrences
Poaceae	*Paspalum*	*lineare*	2634	213	21.50	13.18
Poaceae	*Mesosetum*	*cayennense*	1787	213	14.59	13.18
Poaceae	*Elyonurus*	*muticus*	1431	70	11.68	4.33
Poaceae	*Andropogon*	*lateralis*	677	65	5.53	4.02
Poaceae	*Leptocoryphium*	*lanatum*	633	25	5.17	1.55
Poaceae	*Paspalum*	*geminiflorum*	496	36	4.05	2.23
Cyperaceae	*gen_indet.*	*sp.9*	440	149	3.59	9.22
Eriocaulaceae	*Syngonanthus*	*nitens*	313	110	2.56	6.81
Poaceae	*Paspalum*	*sp.2*	311	38	2.54	2.35
Poaceae	*gen_indet.*	*sp.c_p_b*	285	46	2.33	2.85
Cyperaceae	*Rhynchospora*	*hirta*	197	73	1.61	4.52
Cyperaceae	*Rhynchospora*	*confinis*	196	60	1.60	3.71
Poaceae	*Axonopus*	*canescens*	175	27	1.43	1.67
Malpighiaceae	***Banisteriopsis***	***pubipetala***	**152**	**5**	**1.24**	**0.31**
Annonaceae	***Annona***	***excellens***	**148**	**6**	**1.21**	**0.37**
Poaceae	*Trachypogon*	*plumosus*	146	28	1.19	1.73
Poaceae	*Aristida*	*humeda*	139	11	1.13	0.68
Xyridaceae	*Abolboda*	*ciliata*	123	44	1.00	2.72
Xyridaceae	*Xyris*	*goyazensis*	109	65	0.89	4.02
Sterculiaceae	***Melochia***	***spicata***	**99**	**22**	**0.81**	**1.36**
Myrtaceae	*Myrcia*	*subsessilis*	90	1	0.73	0.06
Flacourtiaceae	***Casearia***	***arborea***	**89**	**9**	**0.73**	**0.56**
Nyctaginaceae	***Neea***	***theifera***	**85**	**2**	**0.69**	**0.12**

Table 5.6. Continued overleaf.

Poaceae	*Panicum*	*parviflorum*	81	31	0.66	1.92
Pterophyta	*Adiantum*	*serratodentatum*	67	12	0.55	0.74
Dilleniaceae	*Curatella*	*americana*	65	2	0.53	0.12
Poaceae	*Gymnopogon*	*fastigiatus*	65	24	0.53	1.49

Table 5.6. Species in the FT plot with a % of total cover greater than 0.5%. The taxa in bold are those which are absent from the modern pollen rain of the site.

5.5. Results

Full pollen counts are available in the appendix, along with the errors associated with these counts. A summary of the results is given below.

5.5.1. TO1 - Seasonally-inundated savanna

The average pollen rain of this site (figure 5.6) is dominated by Moraceae/Urticaceae (24.69%), Cyperaceae (22.35%), Poaceae (18.81%), *Cecropia* (8.70%), *Alchornea* (4.03%), Asteraceae (3.95%), Combretaceae/Melastomataceae (2.75%), *Celtis* (1.78%), *Trema* (1.14%) and *Chamaesyce* (1.03%). However, these major taxa show considerable variability across the site. For example, the minimum percentage of Moraceae/Urticaceae is 17.00% and the maximum 41.33%. Poaceae and Cyperaceae also show similar patterns of high intra-site and inter-annual variability with minima of 3.33% and 7.00% respectively and maxima of 50.17% and 31.00% respectively.

5.5.2. FC1 – Upland savanna

The average pollen rain of this site (figure 5.6) is dominated by Moraceae/Urticaceae (35.06%), Poaceae (29.56%), *Alchornea* (6.12%), *Cecropia* (4.13%), *Celtis* (2.95%), Combretaceae/Melastomataceae (2.90%), Cyperaceae (2.84%), *Borreria* type 1 (2.42%), *Euterpe* type (1.56%) and *Trema* (1.37%).

5.5.3. FT – Seasonally-inundated savanna

The average pollen rain of this site (figure 5.6) is dominated by Moraceae/Urticaceae (36.72%), Poaceae (20.10%), *Alchornea* (7.66%), *Cecropia* (7.03%), Cyperaceae (5.67%), Combretaceae/Melastomataceae (2.98%), *Euterpe* type (2.59%), *Schefflera* (2.28%), *Celtis* (2.20%) and Pterophyta - trilete (2.08%).

5.5.4. MV1 - Seasonally-inundated SDTF

These samples were dominated by *Cecropia* (figure 5.8), which is a pioneer tree and habitat generalist that occurs in a diverse number of neotropical ecosystems (Killeen and Schulenberg, 1998). It is known to be a prolific pollen producer (Bush and Riveria, 1998). In order to observe the other pollen taxa present within this site,

which would potentially have greater application to the palynological characterisation of this ecosystem, it was decided to remove *Cecropia* pollen from the pollen sum so that 300 non-*Cecropia* pollen grains were counted instead. *Cecropia* pollen is very variable across the site with a maximum of over 2000% of the pollen sum at one trap (i.e. with a pollen sum of 300 non-*Cecropia* pollen grain, over 6000 *Cecropia* grains were observed) and a minimum of 3.01% of the pollen sum at another trap (T37-01).

Once *Cecropia* is removed from the pollen sum, the average pollen rain of this site is dominated by Moraceae/Urticaceae (39.00%), unknown type df 61 (6.41%), Asteraceae (6.32%), *Celtis* (6.03%), *Physocalymma scaberrimum* (4.90%), *Doliocarpus* (3.58%), unknown type df 80 (3.12%), Combretaceae/Melastomataceae (2.42%), Poaceae (2.07%) and *Alchornea* (2.00%). Again, there is considerable variability in the major taxa across the site, for example, pollen of *Doliocarpus* and Asteraceae is highly variable across the sites with minima of 0% and maxima of 29.37% and 25.66% respectively. Other major taxa such as *Celtis* have more consistent pollen percentages across the pollen traps.

5.5.5. CP1 - Upland SDTF

The average pollen rain of this site (figure 5.8) is dominated by Moraceae/Urticaceae (25.84%), *Cecropia* (10.49%), *Acalypha* (7.61%), Combretaceae/Melastomataceae (6.66%), *Sebastiania* (4.60%), *Trema* (3.57%), Pterophyta - trilete (3.48%), *Celtis* (3.32%), *Anadenanthera* (2.87%) and unknown type df 40 (2.51%). Both *Sebastiania* and *Phyllanthus acuminatus* have very variable profiles, with minima of 0% and maxima of 21.93% and 9.51% respectively. The high mean of unknown type df 40 is driven by a very high abundance in one trap (T67-00 = 23.13%)

5.5.6. Beni Basin lake sediment results

The average pollen spectra of the lakes were calculated using the mean of the three samples collected from each lake (figure 5.10). The surface lake sediments of all the lakes from the seasonally-inundated savannas of the Beni Basin were dominated by Poaceae and Cyperaceae pollen, which together represent at least 59% of the pollen

sum. Other notable taxa are Moraceae/Urticaceae, which ranges from 5.54% in Laguna Azul to 14.22% in Laguna Cernandez, and Asteraceae, which ranges between 4% and 6% of the pollen sum for all the lakes. Small amounts of tree pollen from *Celtis, Anadenanthera* and *Gallesia* are also present.

5.5.7. SDTF lake sediment results

Four surface samples were analysed from Laguna La Gaiba and the results presented below are the average of these four cores (figure 5.10). These samples were counted by Bronwen Whitney at the University of Edinburgh (B. Whitney, unpublished data). The dominant taxa in this lake were Poaceae (39.94%), Cyperaceae (20.38%), Moraceae/Urticaceae (9.44%), *Acalypha* (4.47%), *Anadenanthera* (4.31%), *Cecropia* (3.33%), *Alchornea* (2.39%), *Celtis* (1.56%), Combretaceae/Melastomataceae (1.42%) and Fabaceae – Mimosoideae type 1 (1.41%).

Three cores were analysed from Laguna Mandioré and the results listed are the average of these cores The dominant taxa in this lake were Poaceae (67.52%), Cyperaceae (12.49%), Moraceae/Urticaceae (3.54%), *Alchornea* (2.71%), *Anadenanthera* (2.19%), unknown type df88 (1.77%), *Celtis* (1.46%), *Cecropia* (1.04%), *Acalphya* (0.83%) and *Trema* (0.73%).

Only one surface core was taken from Laguna Socorros. The dominant taxa were Poaceae (30.77%), *Gallesia* (16.99%), Cyperaceae (11.86%), Moraceae/Urticaceae (6.09%), *Anadenanthera* (5.45%), *Cecropia* (3.85%), unknown type df88 (2.88%), unknown type 103 (2.57%), *Acalypha* (1.60%) and Asteraceae (1.28%).

5.5.8. Pollen accumulation rates

The pollen accumulation rates of individual taxa from the sites in NKMNP are displayed in figures 5.7 and 5.9 and the annual pollen accumulation rates of the sites are tabulated in table 5.7. The pollen accumulation rates of individual taxa in the surface lake sediments are displayed in figure 5.11.

5.5.9. Pollen/vegetation relationships

Palynologically silent taxa (those not found in the modern pollen rain) are identified in tables 5.3, 5.4, 5.5 and 5.6 by the bold font; the taxa in normal font are those which are found in the modern pollen rain. The pollen/vegetation ratios are presented for all pollen taxa that have a maximum abundance of ≥1% in any one pollen trap (tables 5.8, 5.9, 5.10 and 5.11).

5.5.10. Moraceae/Urticaceae differentiation of NKMNP pollen traps

Fifty Moraceae/Urticaceae pollen grains were counted from six traps from each site and the results are given in figure 5.12.

5.5.11. Comparison between pollen signals from artificial pollen traps and surface lake sediments

The results from figure 5.13 show that all the surface lake sediment samples plot together as a cluster in the centre of the diagram, separated by the savanna pollen trap samples to the left and the SDTF pollen traps samples to the right

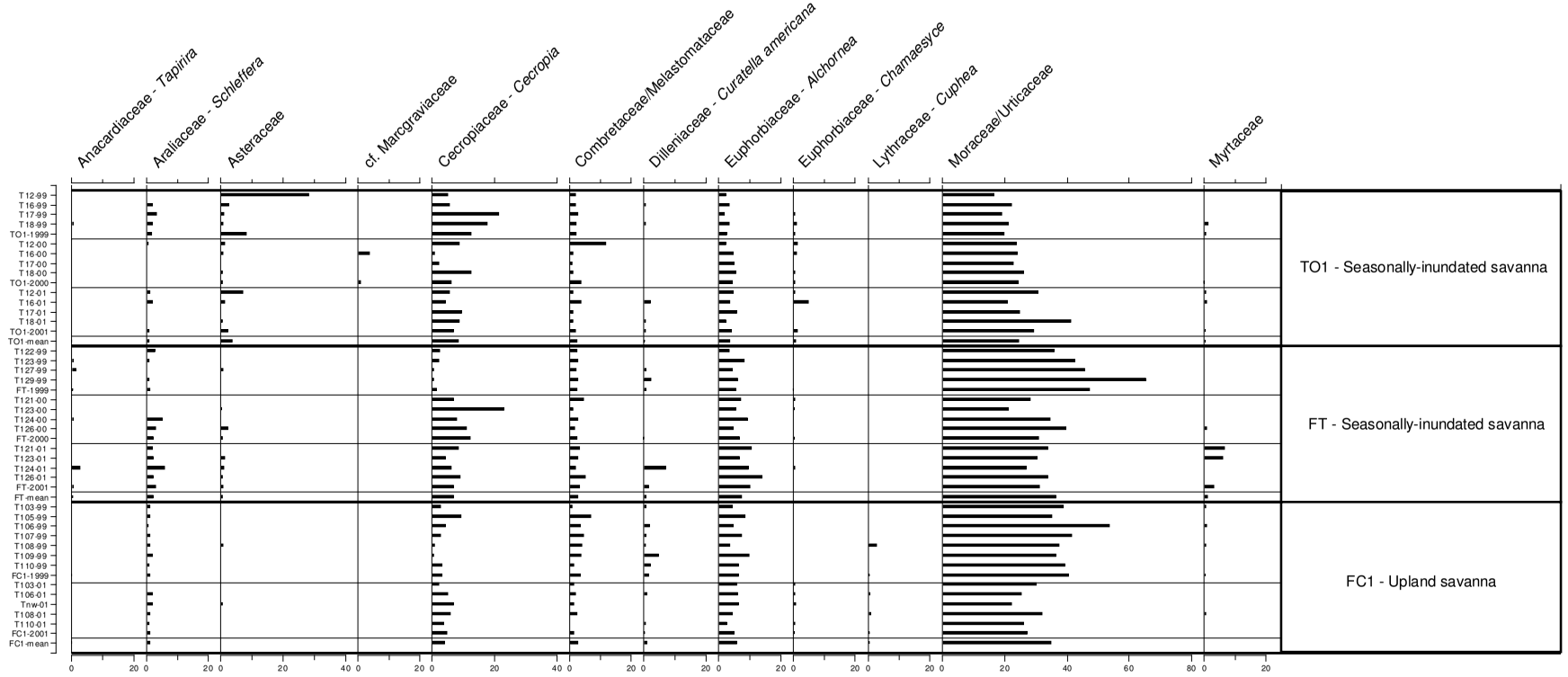

Figure 5.6. Continued overleaf.

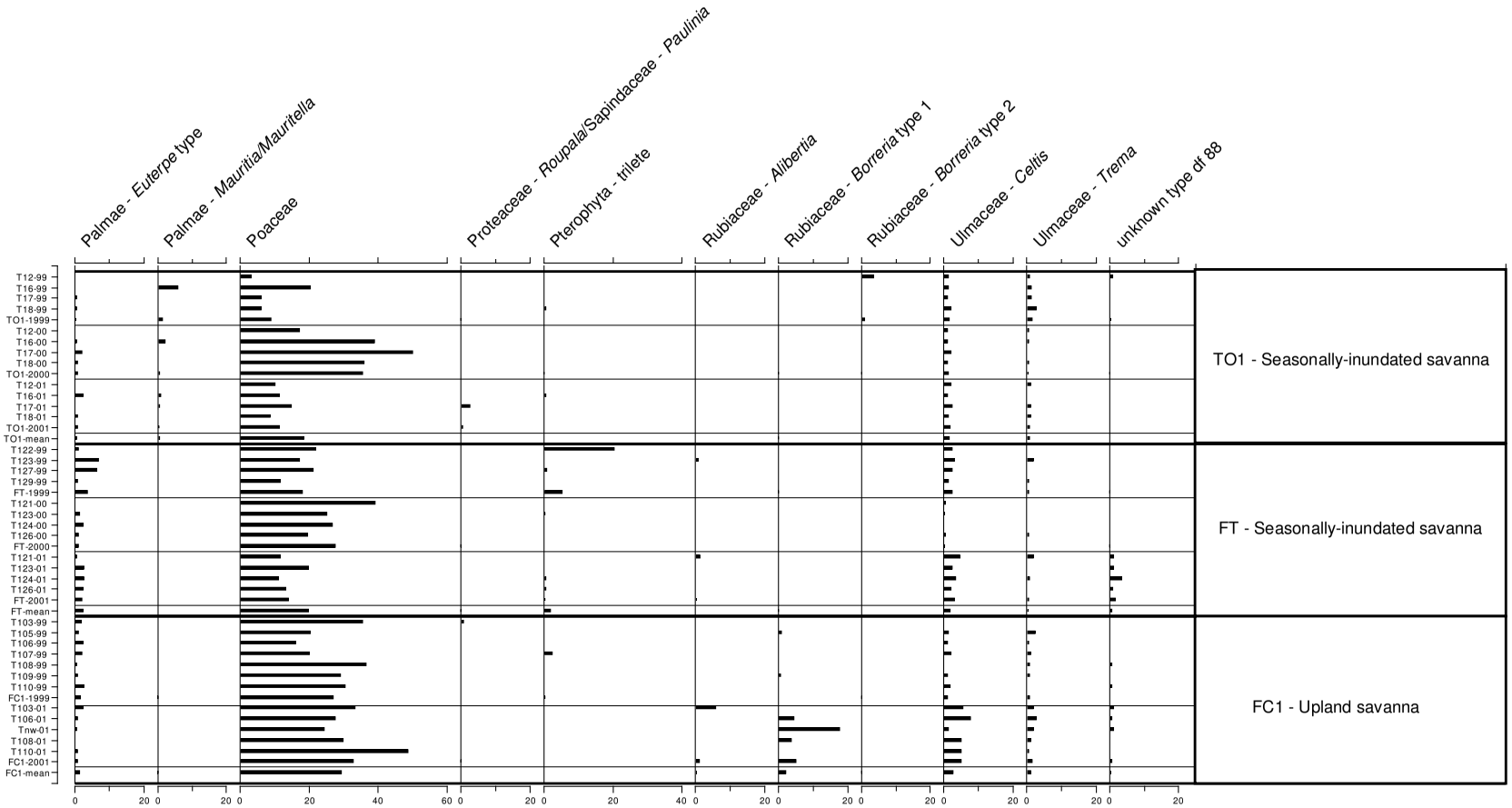

Figure 5.6. Pollen percentage diagram for savanna sites within NKMNP showing all taxa with a maximum percentage ≥3% in any one sample. For the sample codes, Txx-yy is plot code for a pollen trap (e.g T12-99), "site code-year" is the average pollen rain of a site for the sampling year described e.g. (TO1-1999) and "site code-mean" (e.g. TO1-mean) is the mean pollen rain for the ecosystem over the sampling period

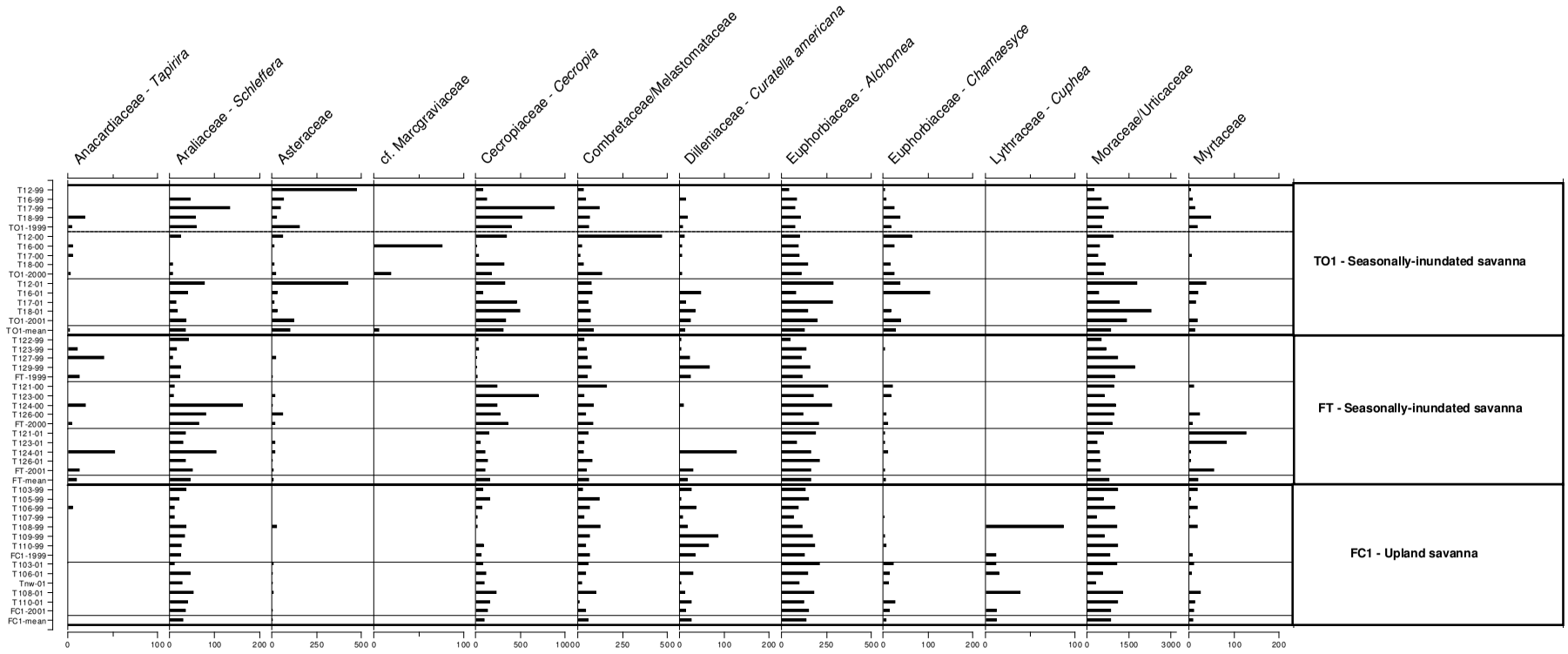

Figure 5.7. Continued overleaf.

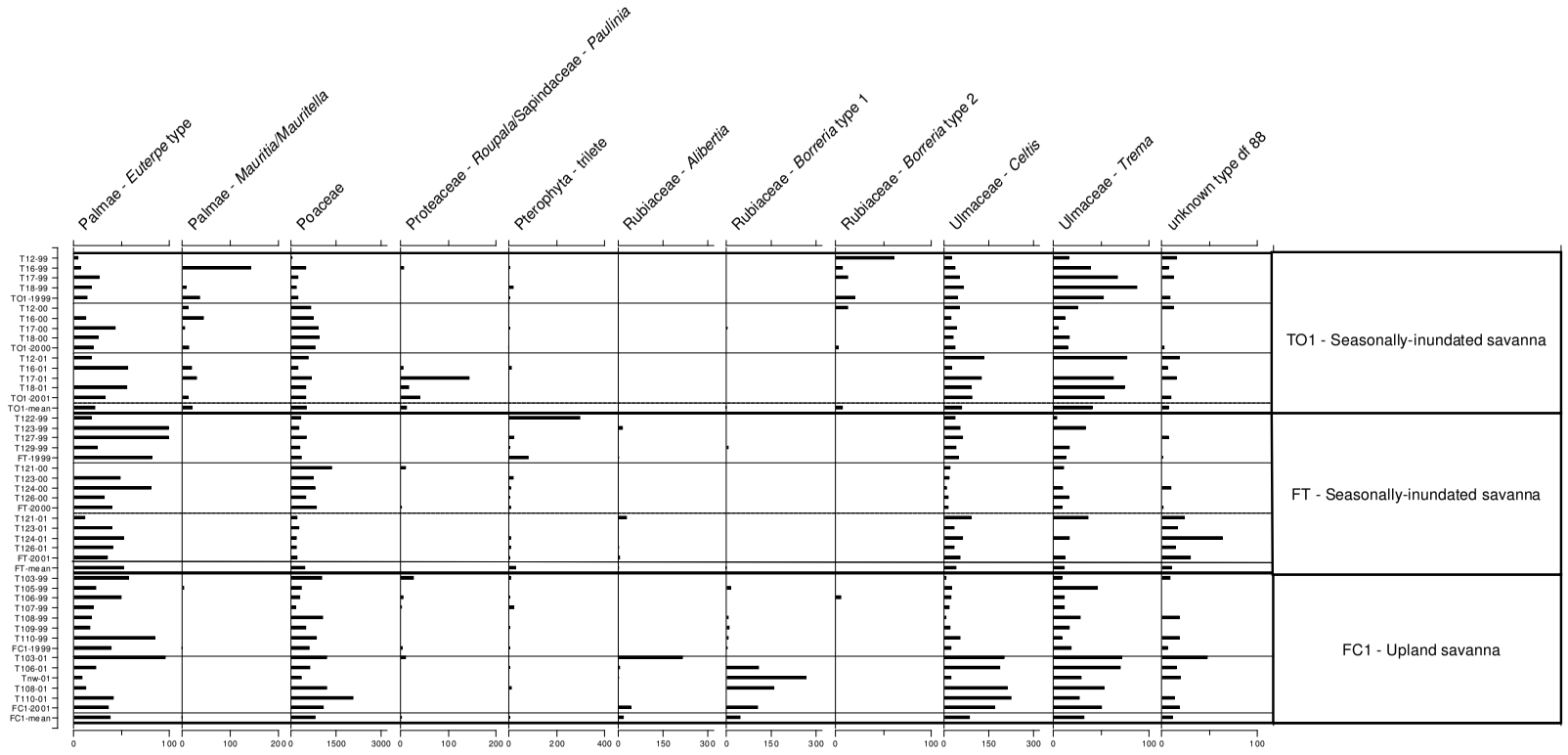

Figure 5.7. Pollen accumulation rates (grains cm^{-2} yr^{-1}) for the savanna pollen traps showing all taxa with a maximum percentage ≥3% in any one sample. For the sample codes, Txx-yy is plot code for a pollen trap (e.g T12-99), "site code-year" is the average pollen rain of a site for the sampling year described e.g. (TO1-1999) and "site code-mean" (e.g. TO1-mean) is the mean pollen rain for the ecosystem over the sampling period. For details of the calculation of pollen accumulation rates, see section 5.3.

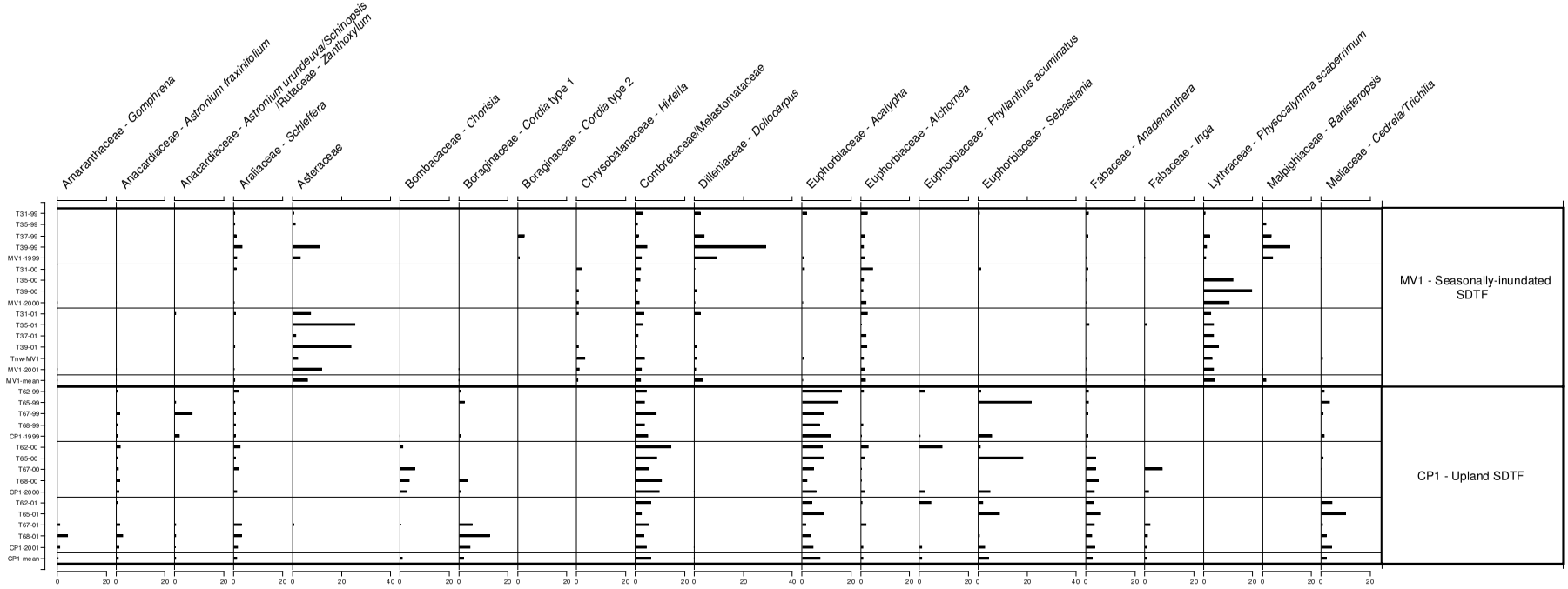

Figure 5.8. Continued overleaf.

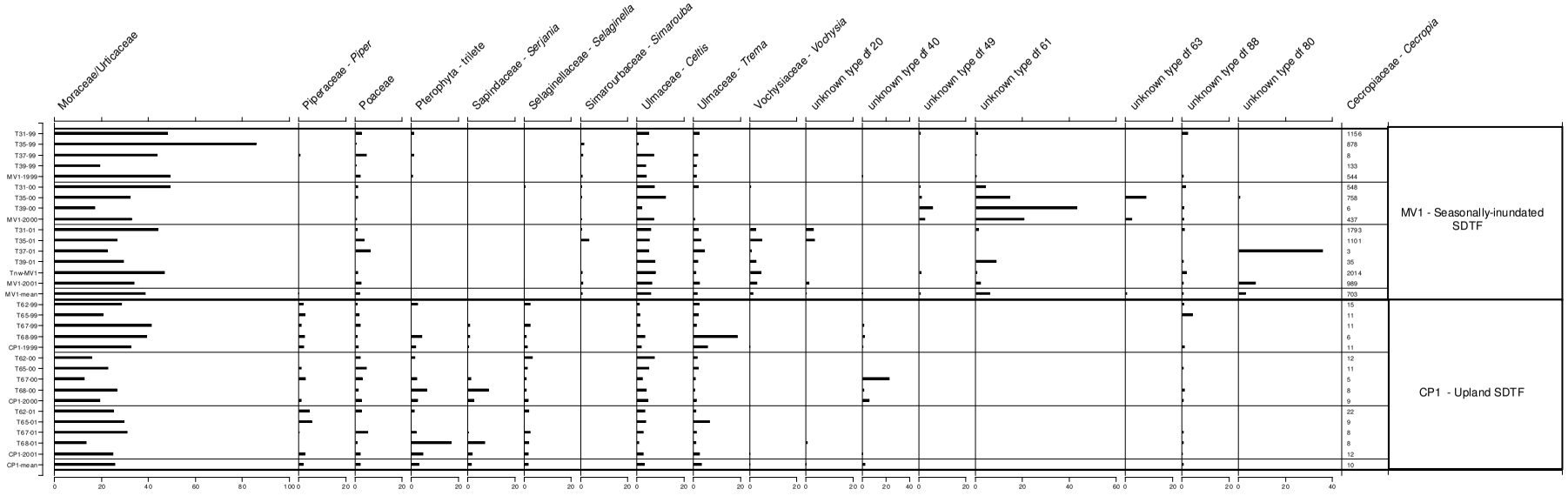

Figure 5.8. Pollen percentage diagram for the SDTF pollen traps showing all taxa with a maximum percentage ≥3% in any one sample. For the sample codes, Txx-yy is plot code for a pollen trap (e.g T12-99), "site code-year" is the average pollen rain of a site for the sampling year described e.g. (TO1-1999) and "site code-mean" (e.g. TO1-mean) is the mean pollen rain for the ecosystem over the sampling period. Note for the seasonally-inundated SDTF site, *Cecropia* is excluded from the pollen sum and values are presented as % of the sum. For the upland SDTF, *Cecropia* is included within the pollen sum.

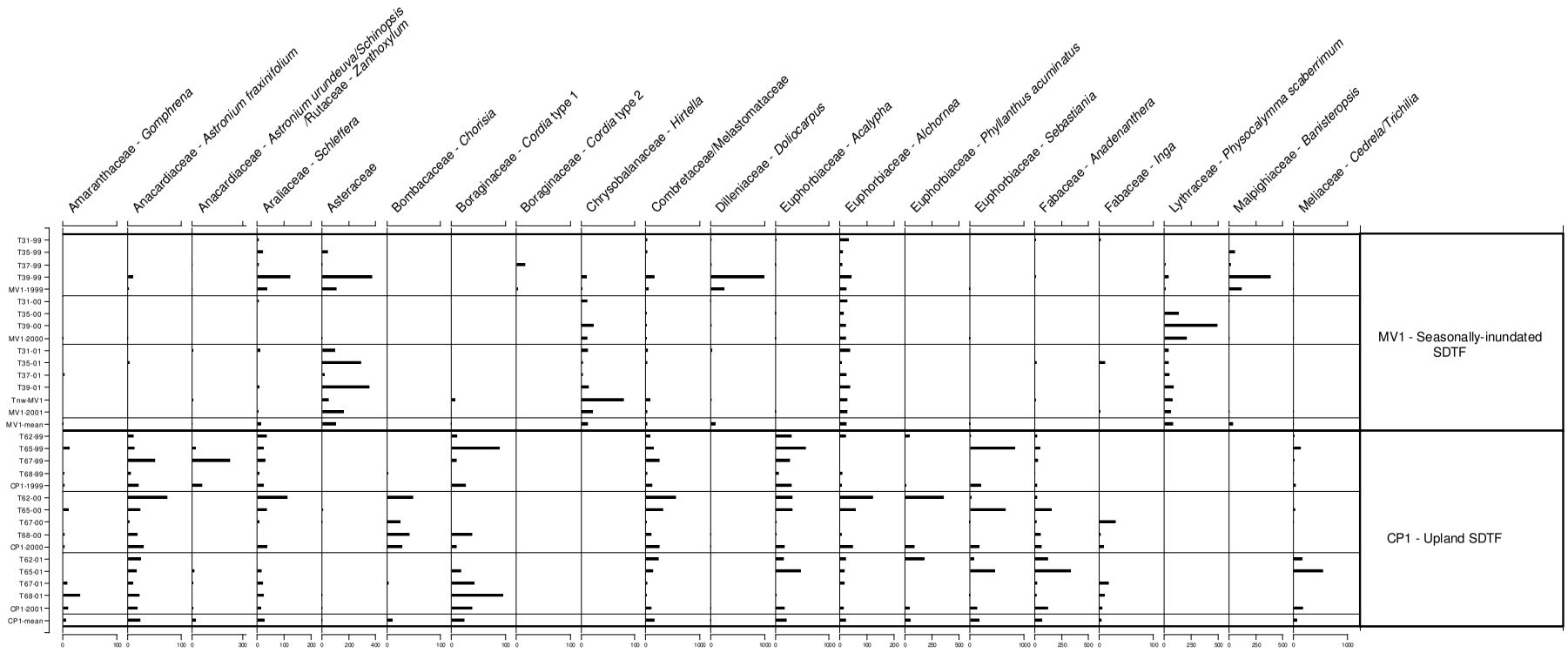

Figure 5.9. Continued overleaf.

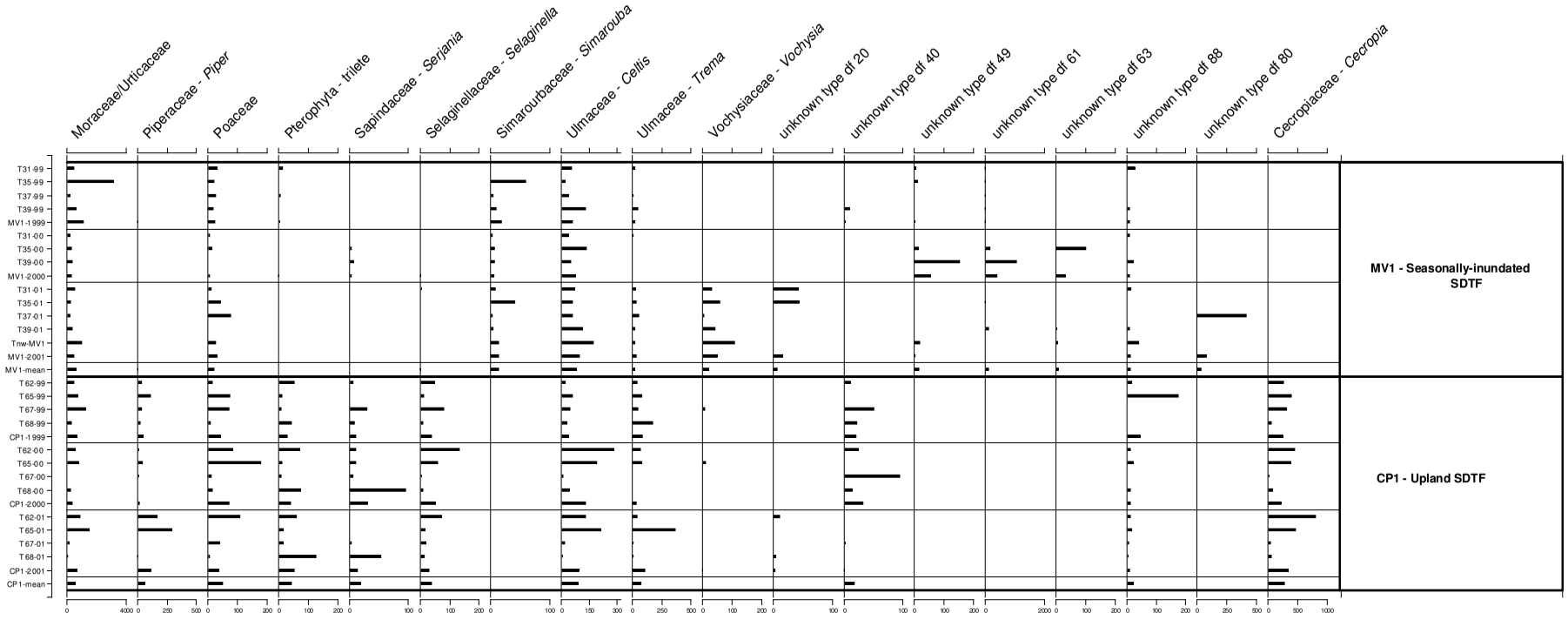

Figure 5.9. Pollen accumulation rates (grains cm^{-2} yr^{-1}) of taxa for the SDTF pollen traps showing all taxa with a maximum percentage ≥3% in any one sample. For the sample codes, Txx-yy is plot code for a pollen trap (e.g T12-99), "site code-year" is the average pollen rain of a site for the sampling year described e.g. (TO1-1999) and "site code-mean" (e.g. TO1-mean) is the mean pollen rain for the ecosystem over the sampling period. Note that pollen accumulation rates are not displayed for *Cecropia* pollen within the MV1 site as the severe-overepresentation of it within these pollen traps mean the pollen accumulation rates could not be reliable calculated. For details of the calculation of pollen accumulation rates, see section 5.3.

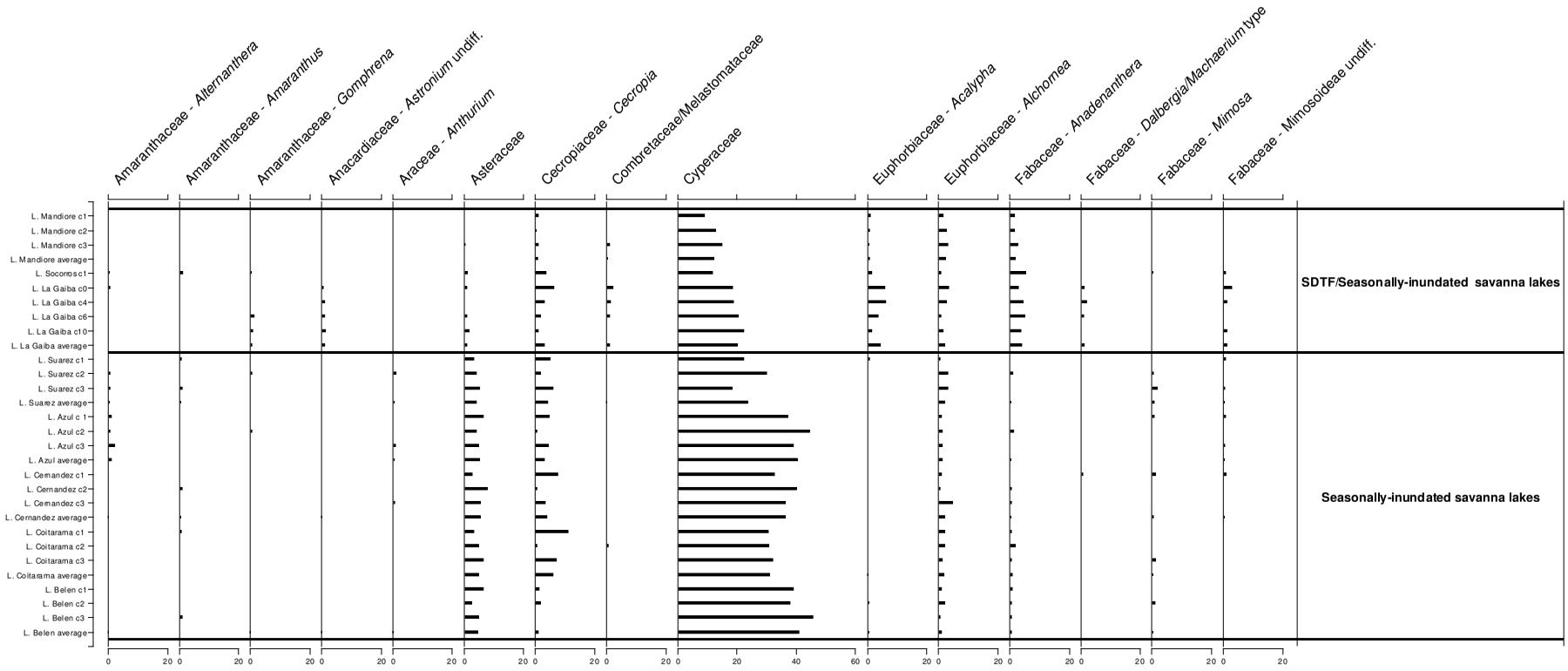

Figure 5.10. Continued overleaf.

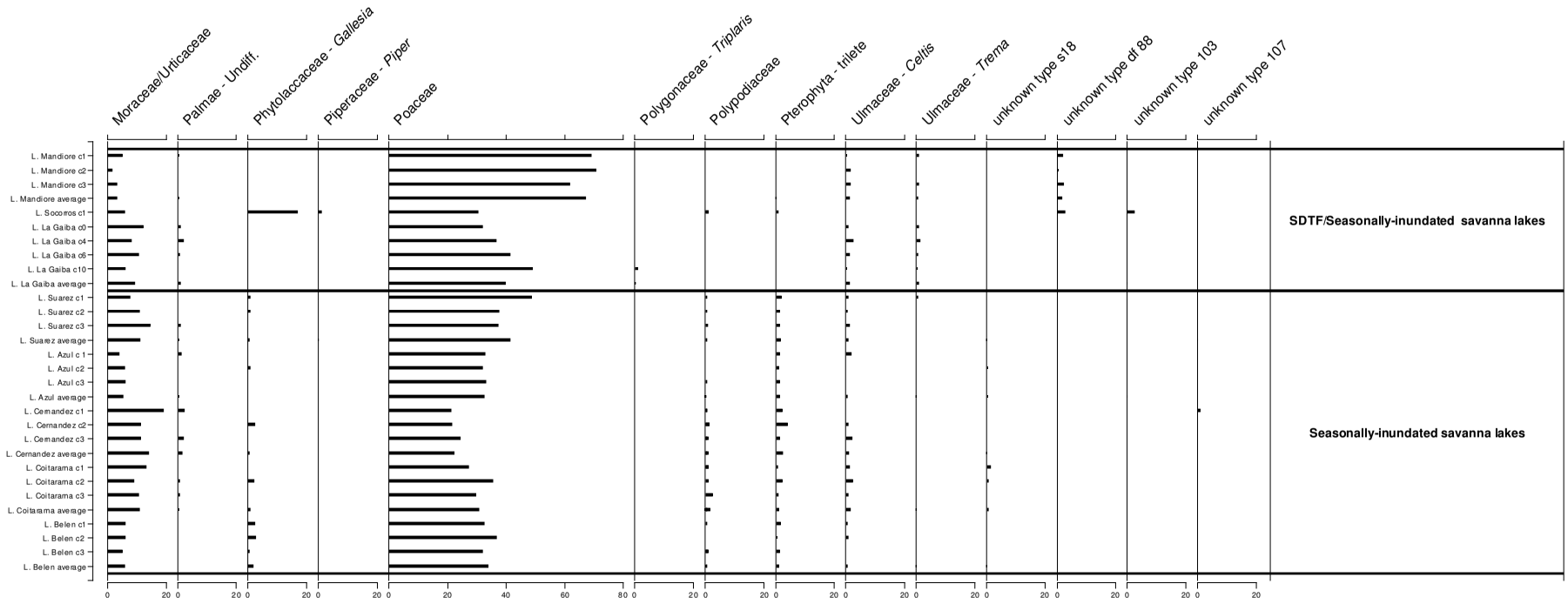

Figure 5.10. Percentage pollen diagram of lake sediment data showing all taxa with a maximum percentage of ≥1% in any one sample.

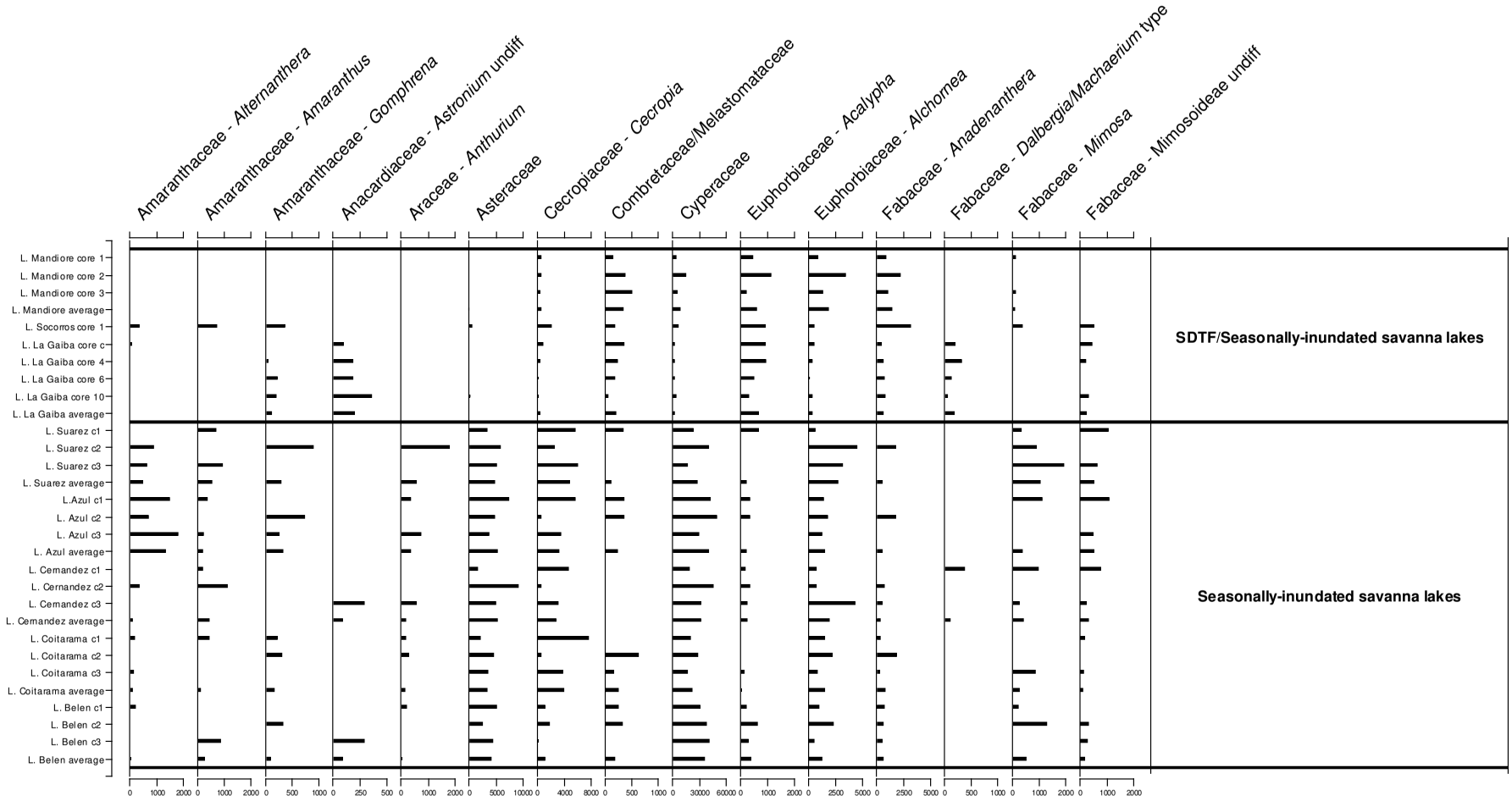

Figure 5.11. Continued overleaf.

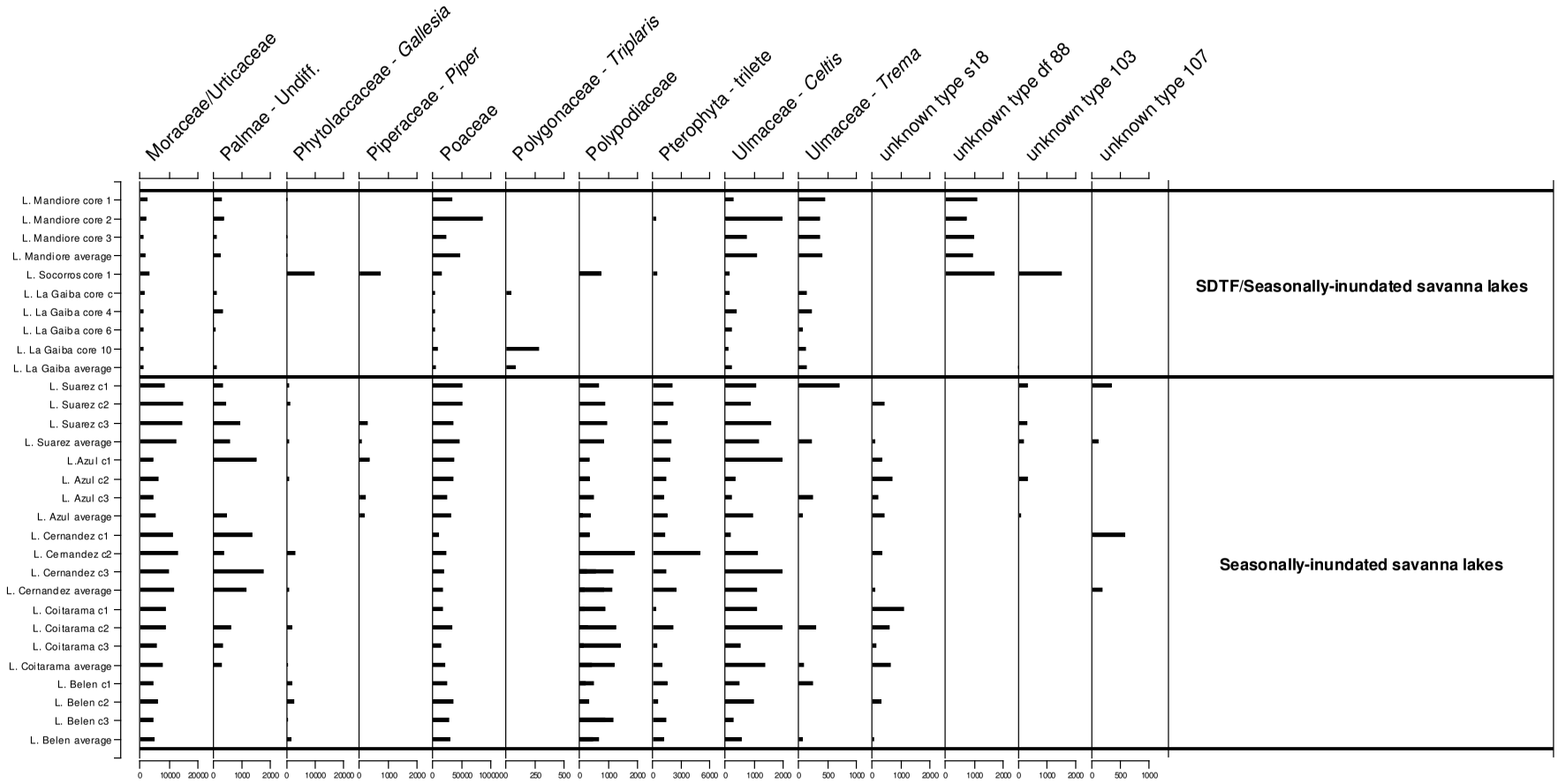

Figure 5.11. Pollen concentration diagram(grains cm^{-3}) of lake sediment data showing all taxa with a maximum percentage of ≥1% in any one sample. For details of the calculation of pollen concentration, see section 5.3.

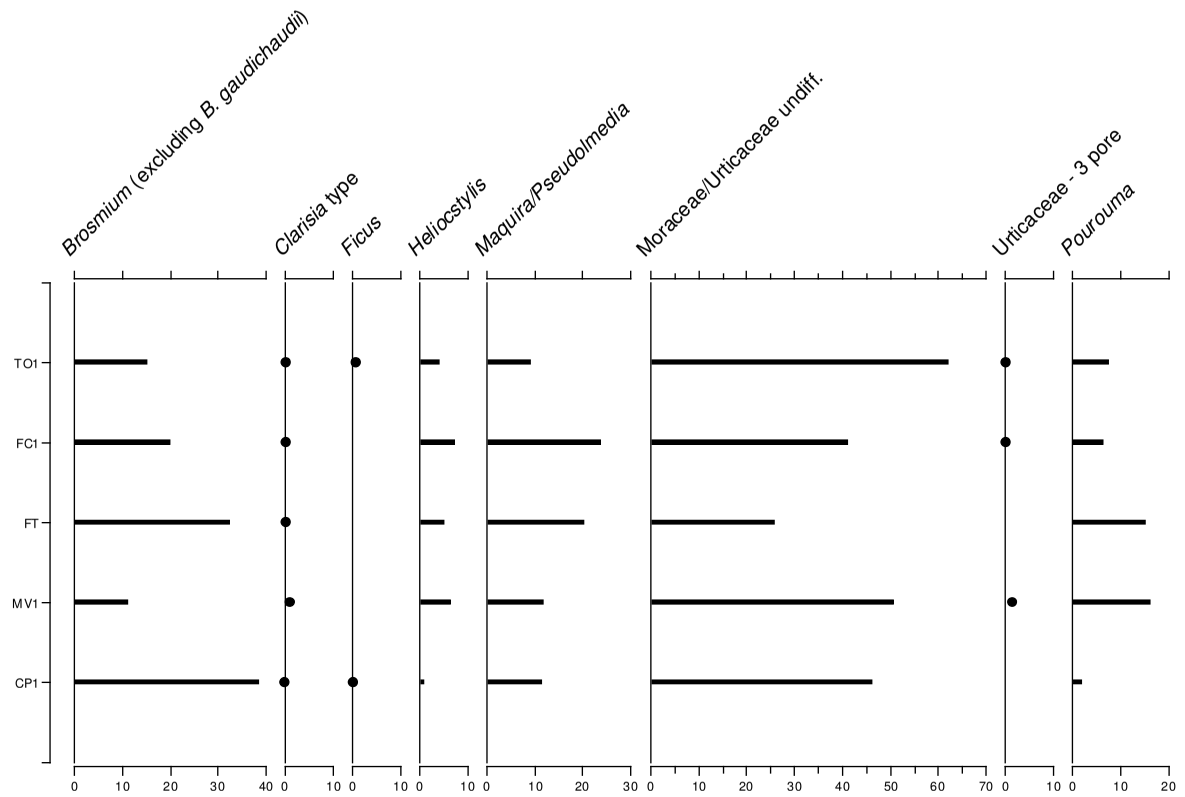

Figure 5.12. Moraceae/Urticaceae differentiation within the pollen traps from NKMNP. Results are presented as percentages of the total Moraceae/Urticaceae sum.

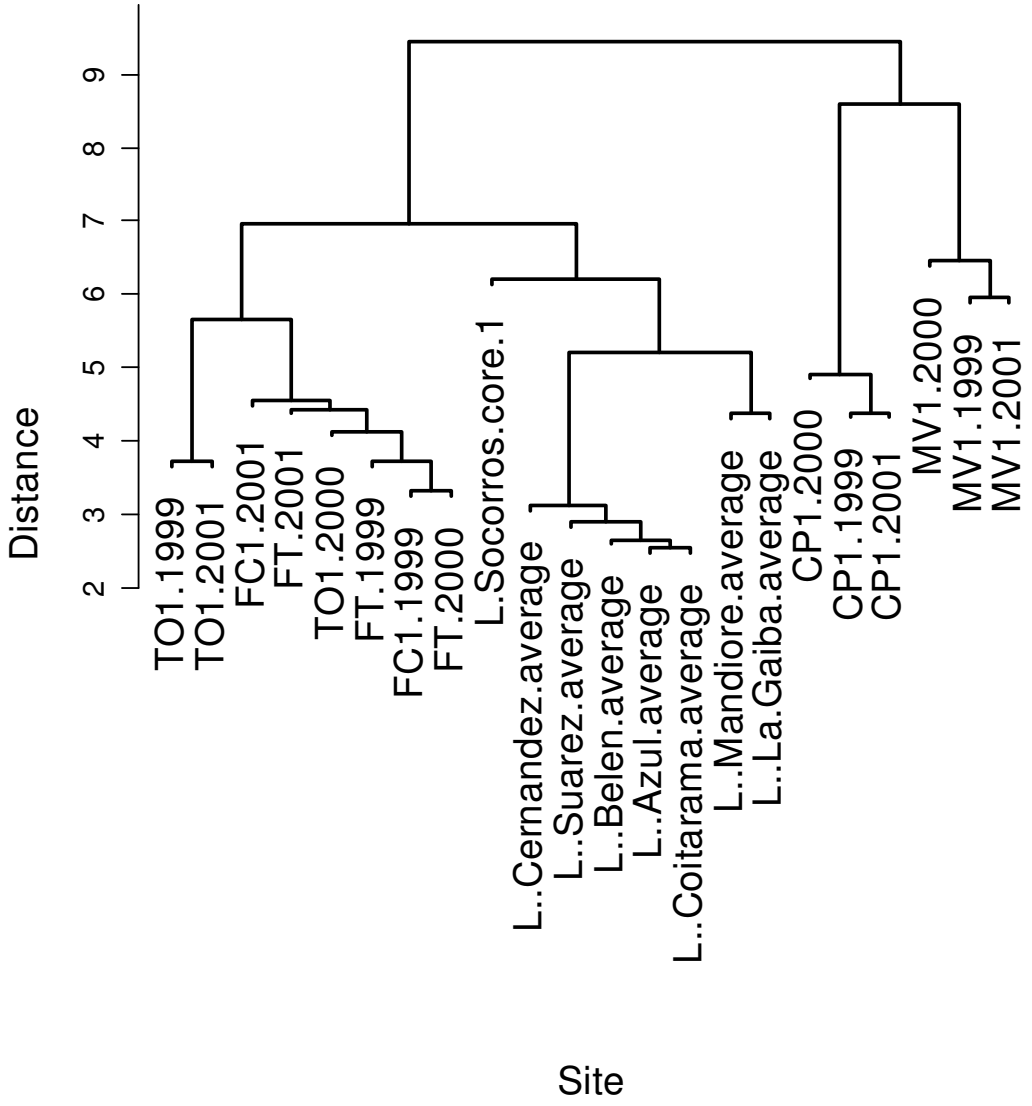

Figure 5.13. Cluster dendrogram of modern pollen rain from the surface lake sediments and artificial pollen traps. The lake samples have the code "L..name", e.g. "L..Cernandez.average". The pollen traps have the code "sitecode.year", e.g. "TO1.1999".

Site	Pollen accumulation rates (grains cm^{-2} yr^{-1})	1 standard deviation
TO1, seasonally-inundated savanna – 1999	2780	1009
TO1, seasonally-inundated savanna – 2000	2598	971
TO1, seasonally-inundated savanna – 2001	4612	1714
TO1, seasonally-inundated savanna - mean	**3330**	**1496**
FC1, upland savanna – 1999	2143	782
FC1, upland savanna – 2001	3150	1177
FC1, upland savanna – mean	**2563**	**1052**
FT, seasonally-inundated savanna – 1999	2066	580
FT, seasonally-inundated savanna – 2000	3030	410
FT, seasonally-inundated savanna – 2001	1615	226
FT, seasonally-inundated savanna – mean	**2237**	**729**
MV1, seasonally-inundated SDTF – 1999	2194	1588
MV1, seasonally-inundated SDTF – 2000	1393	982
MV1, seasonally-inundated SDTF - 2001	1461	429
MV1, seasonally-inundated SDTF – mean	**1689**	**1035**
CP1, upland SDTF – 1999	2437	1278
CP1, upland SDTF – 2000	2231	1731
CP1, upland SDTF – 2001	2635	2277
CP1, upland SDTF – mean	**2435**	**1645**

Table 5.7. Pollen accumulation rates of the pollen traps from NKMNP. Note *Cecropia* pollen has been removed from the pollen accumulation rate calculations for the MV1 site.

Taxa	Pollen mean (%)	% of total stems in the vegetation plot	p/v ratio	Flower structure	Pollination mechanism
Moraceae/Urticaceae	39.00	6.66	5.86	Unisexual	A/E
unknown type df 61	6.41	-	-	-	-
Asteraceae	6.32	0.00	Absent in vegetation inventory	Bisexual or unisexual	E
Celtis	6.03	0.00	Absent in vegetation inventory	Unisexual or bisexual	A
Physocalymma scaberrimum	4.90	13.43	0.36	Bisexual	E
Doliocarpus	3.58	0.46	7.78	Bisexual	E
unknown type df 80	3.12	-	-	-	-
Combretaceae/ Melastomataceae	2.42	2.18	1.11	Bisexual, sometimes unisexual	E
Poaceae	2.07	0.00	Absent in vegetation inventory	Bisexual or unisexual	A
Alchornea	2.00	0.11	18.18	Unisexual	A
Trema	1.90	0.00	Absent in vegetation inventory	Unisexual	A
Vochysia	1.52	0.34	4.47	Bisexual	E
Banisteriopsis	1.51	0.57	2.65	Bisexual	E

Table 5.8. P/V ratios and pollination strategy for all pollen taxa in the MV1 site with a mean ≥1%. A = anemphilous (wind-pollinated), E = entomophilous (insect-pollinated). References: Berg (2004a), Berg (2004b), Prusti and Saneto (2004), Bush (1995), Graham *et al.* (1985), Stace (2004), Renner (2004) and Davis (2004).

Taxa	Pollen mean (%)	% of total stems in the vegetation plot	p/v ratio	Flower structure	Pollination mechanism
Moraceae/Urticaceae	25.84	0.63	41.02	Unisexual	A/E
Cecropia	10.49	0.00	Absent in vegetation inventory	Unisexual	A
Acalypha	7.61	0.00	Absent in vegetation inventory	Unisexual	A
Combretaceae/Melastomataceae	6.66	17.46	0.38	Bisexual, sometimes unisexual	E
Sebastiania	4.60	3.17	1.45	Unisexual	E
Trema	3.57	0.00	Absent in vegetation inventory	Unisexual	A
Pterophyta	3.48	0.00	Absent in vegetation inventory	-	-
Celtis	3.32	0.00	Absent in vegetation inventory	Unisexual or bisexual	A
Anadenanthera	2.87	7.94	0.36	Bisexual	E
Unknown type df 40	2.51	-	-	-	-
Poaceae	2.36	0.00	Absent in vegetation inventory	Bisexual or Unisexual	A
Cedrela/Trichilia	2.24	0.63	3.56	Unisexual	E
Cordia type 1	2.15	0.79	2.72	Bisexual	E

Table 5.9. Continued overleaf.

Piper	2.13	0.00	Absent in vegetation inventory	Bisexual	E
Serjania	1.79	0.00	Absent in vegetation inventory	Bisexual or unisexual	E
Selaginella type	1.75	0.00	Absent in vegetation inventory	-	-
Schefflera	1.52	0.00	Absent in vegetation inventory	Bisexual	E
Phyllanthus acuminatus	1.43	0.00	Absent in vegetation inventory	Unisexual	E
Astronium fraxinifolium	1.18	0.63	1.87	Unisexual	E
Chorisia	1.03	0.32	3.22	Bisexual	E
Alchornea	1.03	0.00	Absent in vegetation inventory	Unisexual	A

Table 5.9. P/V ratios and pollination strategy for all pollen taxa in the CP1 site with a mean ≥1%. A = anemphilous (wind-pollinated), E = entomophilous (insect-pollinated). References: Berg (2004a), Berg (2004b), Bush (1995), Stace (2004), Renner (2004), Jardim *et al.* (2003), Davis (2004), Alverson (2004).

Taxa	Pollen mean (%)	% cover in vegetation plot	p/v ratio	Flower structure	Pollination mechanism
Moraceae/Urticaceae	35.06	0.94	37.29	Unisexual	A/E
Poaceae	29.56	51.01	0.58	Bisexual or unisexual	A
Alchornea	6.12	0.00	Absent in vegetation inventory	Unisexual	A
Cecropia	4.13	0.00	Absent in vegetation inventory	Unisexual	A
Celtis	2.95	0.00	Absent in vegetation inventory	Unisexual or bisexual	A
Combretaceae/Melastomataceae	2.90	0.03	96.67	Bisexual, sometimes unisexual	E
Cyperaceae	2.84	0.24	11.83	Bisexual or unisexual	A
Borreria type 1	2.42	4.88	0.50	Bisexual	E
Euterpe type	1.56	0.00	Absent in vegetation inventory	Unisexual	E
Trema	1.37	0.00	Absent in vegetation inventory	Unisexual	A
Schefflera	1.31	0.00	Absent in vegetation inventory	Bisexual	E
Curatella americana	1.25	0.07	17.86	Bisexual	E

Table 5.10 P/V ratios and pollination strategy for all pollen taxa in the FC1 site with a mean ≥1. A = anemphilous (wind-pollinated), E = entomophilous (insect-pollinated). References: Berg (2004a), Berg (2004b), Davis (2004), Bush (1995), Stace (2004), Renner (2004), Thomas (2004) and Ramirez (2004).

Taxa	Pollen mean (%)	% cover in the vegetation	p/v ratio	Flower structure	Pollination mechanism
Moraceae/Urticaceae	36.72	0.00	Absent in vegetation inventory	Unisexual	A/E
Poaceae	20.10	74.93	0.27	Bisexual or unisexual	A
Alchornea	7.66	0.16	47.88	Unisexual	A
Cecropia	7.03	0.49	14.35	Unisexual	A
Cyperaceae	5.69	7.13	0.80	Unisexual	A
Combretaceae/Melastomataceae	2.98	0.63	4.73	Bisexual, sometimes unisexual	E
Euterpe type	2.59	0.00	Absent in vegetation inventory	Unisexual	E
Schefflera	2.28	0.49	4.65	Bisexual	E
Celtis	2.20	0.00	Absent in vegetation inventory	Unisexual or bisexual	A
Pterophyta - trilete	2.08	0.55	3.78	N/A	N/A
Myrtaceae	1.28	1.10	1.16	Bisexual	E
Curatella americana	1.00	0.53	1.89	Bisexual	E

Table 5.11. P/V ratios and pollination strategy for all pollen taxa in the FT site with a mean ≥1%. A = anemphilous (wind-pollinated), E = entomophilous (insect-pollinated). References: Berg (2004a), Berg (2004b), Bush (1995), Thomas (2004), Stace (2004), Renner (2004), Kawosaki and Holst (2004) and Ramirez (2004).

5.6. Discussion

5.6.1. Modern pollen rain from savanna ecosystems

The Beni Basin lake samples (figure 5.10) are dominated by Poaceae and Cyperaceae pollen (over 50% of the pollen sum for all samples), which reflects the open nature of these savannas, with grass-dominated landscapes and marshes (*bajios*) covered by *Cyperus giganteus.* Although it is not possible to differentiate pollen from aquatic grasses from that of grasses growing on dry land, the lakes sampled had only a narrow fringe of aquatic vegetation of which grasses were a fairly minor component; hence it is inferred that the majority of the grass pollen is derived from the savanna ecosystems surrounding the lakes. Asteraceae is also abundant within the samples, with these plants being abundant herb, shrubs and vines in the savannas of the region (Beck and Moraes, 2004).

The dominant tree pollen represented in the samples is from the Moraceae/Urticaceae taxonomic group. At a regional scale, the landscape of the Beni Basin has numerous areas of woody vegetation in gallery forests, fragmented areas of former gallery forests and forest islands. Those which line the main river (Río Mamoré) in the Beni Basin have been placed within the South West Amazonian forest ecoregion (Olson *et al.,* 2001) and are connected to more extensive areas of evergreen forest to the north of the Beni region. The forest component within these samples is characterised by this Moraceae/Urticaeae pollen, which is small, light and very easily dispersed from areas of forest into the surrounding open savanna ecosystems. The Moraceae species, *Brosimum lactescens, Clarisia bifolia, Clarisia racemosa, Pourouma guianensis, Maclura tinctoria* and *Poulsenia armata* are trees of the gallery forests of the Río Mamoré (Beck and Moraes, 2004; Navarro and Maldonado, 2005), whilst the Urticaceae genera *Boehmeria* and *Urera* are shrubs and herbs of these forests. Both families are generally absent from the more open savanna ecosystems of the Beni Basin (Beck and Moraes, 2004), indicating that most of the pollen of this group is of a regional forest nature. Generally the percentage of Moraceae/Urticaceae pollen is

not greater than 20% and this is much lower than the levels obtained from evergreen forest within lowland Bolivia (Gosling *et al.,* 2005; Burn, 2008).

On the non-flooded areas (*alturas)*, semi-deciduous forest and *cerradão* vegetation exists (Navarro and Maldonado, 2005) and trees typical of these environments e.g. *Gallesia* and *Anadenanthera* are also represented within the Beni lake sediments, although at very low abundances (maxima = 1.00% and 1.11% respectively).

Commonly accepted savanna indicators (e.g. *Curatella americana, Byrsonima)* are very rare within the sediments of the Beni lakes, being represented by the occasional grain, despite both taxa being present within the savanna ecosystems of the region. Common trees in the areas which only experience minor or no inundation (*alturas* and *semi-alturas)* such as *Copernicia alba* (Palmae) and *Tabebuia heptaphylla* (Bignoniaceae), are both completely absent from the pollen spectra of any of the lakes under study.

Some studies have shown that pollen spectra within lake sediments can be spatially heterogeneous across a lake body due to differential deposition of pollen grains (Davis *et al.,* 1971). Triplicate cores were taken from all five lakes to allow average pollen spectra for the lake to be calculated and visual comparison of surface pollen spectra from the same lake shows a high degree of similarity between the samples from the same lake (figure 5.10). All lakes sampled were shallow (<2 m depth when sampled) so it is assumed that the water column is well mixed, which would result in a fairly homogenous pollen assemblages within the lake sediments. There was also no notable increase in the abundance of pollen of aquatic/semi-aquatic taxa (e.g. *Eichhornia, Echinodorus, Sagittaria*) towards the margins of the lakes.

The savanna ecosystems at NKMNP (figure 5.6) have surprisingly low percentages of grass pollen (TO1-*pampa termitero* mean = 18.81%, FC1 - *campo cerrado* mean = 29.56%, FT- *pampa termitero* mean = 20.10%). The most likely reason for the low grass pollen signal is as a result of its dilution by pollen of Moraceae/Urticaceae. Species within Moraceae and Urticaceae have much higher abundance values within

evergreen forest ecosystems than within the savanna ecosystems (Killeen and Schulenberg, 1998) and previous studies have shown that the evergreen rainforests of NKMNP have Moraceae/Urticaceae pollen abundances of up to 60% of the pollen sum (Burn, 2008; Gosling *et al.*, 2005). All three savanna sites are very close to evergreen forest/savanna boundaries (<2 km), therefore it is suggested that the majority of the Moracae/Urticaceae pollen is of a regional (evergreen forest) nature. The Moraceae and Urticaceae families have numerous wind-pollinated species (Berg, 2004a, Berg, 2004b) and produce small (<20 µm), light pollen grains, which would be easily dispersed from areas of evergreen forest into the neighbouring savanna ecosystems.

Of the Moraceae/Urticaeae pollen that could be differentiated within these sites (figure 5.12), the evergreen forest genera, *Brosimum* (excluding *B. gaudichaudii*), *Psuedolmedia, Helicostylis, Pourouma* and *Maquira* were observed. The existence of these pollen grains within the pollen traps shows that a large fraction of the Moraceae/Urticaceae pollen can be attributed to a "regional" evergreen forest signal that is being blown into the sites from areas of evergreen forest within close proximity of the traps. *Sorocea guilleminiana* is a Moraceae species that is found within savanna sites, however, it is very difficult to differentiate this taxon from other diporate Moraceae/Urticaceae/Cecropiaceae pollen grains. Any pollen grains of this taxon would have been placed within the Moraceae/Urticaceae undifferentiated category. Therefore, it has to be accepted that some locally produced *Sorocea guilleminiana* pollen may be present within the presumed "regional" Moraceae/Urticaceae pollen signal.

Previously published modern pollen rain studies from the savanna ecosystems of Brazil (Ledru, 2002; Salgado-Labouriau, 1979) found very low quantities of Moraceae/Urticaceae pollen compared to this research. This is believed to be due to the different regional vegetation types surrounding these study sites. The sites in this thesis were all very close to savanna/evergreen forest ecotones (<5 km), whereas those of Salgado-Labouriau (1979) and Ledru (2002) were from the centre of the Cerrado Biome where any areas of evergreen forest are restricted to gallery forests

along watercourses and the landscape is dominated by open savannas. Therefore, there is a much lower possibility of the savanna signal being diluted by pollen types typical of evergreen rainforest.

Previous work upon savanna ecosystems using pollen traps has shown much higher grass concentrations e.g. 74% (Salgado-Labouriau, 1979) or 50% (Ledru, 2002). Bush (2002) asserted that Poaceae concentrations of 50-90% are "strongly indicative of savanna ecosystems" and it can be observed that the grass pollen percentages in the present work are much lower than this. The savanna sites used within this study are located at the ecotone between savanna and evergreen forest (Killeen, 1998). In order to aid comparisons with other modern pollen rain studies from cerrado ecosystems, which were located within the centre of the Cerrado Biome (see previous paragraph) and distant from the Amazon forest-savanna ecotone, it was decided to recalculate the Poaceae percentages if Moraceae/Urticaceae was removed from the pollen sum, as most of the pollen of these families within the savanna samples is believed to be of a regional forest origin (see previous paragraphs). The recalculated Poaceae percentages were 25.08% for the TO1 *pampa termitero* site, 45.41% for the FC1 *campo cerrado* site and 31.97% for the FT *pampa termitero* site. The Poaceae percentage of the *campo cerrado* site is now closer to the value calculated by Ledru (2002) of 50% for this ecosystem within central Brazil. However, the values for all savannas are still lower than the values of 50-90% given by Bush (2002). The lake sediment samples from the savanna/forest mosaic of the Beni Basin also show low Poaceae percentages (<50%).

If Poaceae percentages are fairly low (such as the values of <50% generally observed in this study), then it may be difficult to infer whether the Poaceae signal represents a pollen signal from hydrophytic grasses growing on the lake margins and within the lake or whether it represents the presence of savanna areas around the lake. To aid the interpretation of these records, it appears that in mosaic landscapes (such as the present forest-savanna mosaic of the Beni Basin in Bolivia or the forest-savanna ecotone of NKMNP, Bolivia), it is important to consider the full pollen spectra from the site, as the additional non-Poaceae taxa should give an indication of the extent of

forest upon the landscape. The presence of animal-pollinated forest tree taxa would be a useful indicator of forest within the landscape as their pollen grains are typically poorly dispersed, indicating the presence of trees (and forest) close to the sampling site. Colinvaux *et al.* (1996) indicated that it was the locally produced poorly dispersed animal-pollinated taxa that are important in terms of interpreting the pollen signal as forest. In this setting, any Poaceae signal could be interpreted as representative of aquatic or shore line grasses within a closed forest vegetation formation. In this study the majority of forest pollen captured within the surface lake sediments and the artificial pollen traps was that of wind-pollinated taxa (e.g. Moraceae/Urticaceae, *Cecropia* and *Alchornea*). If the forest signal of a fossil pollen record consists solely of wind-pollinated taxa, then it could be inferred that this is a regional pollen signal (i.e. pollen which has been transported some distance) and that there is only limited forest cover immediately around the sampling site. In this context, the Poaceae signal could be interpreted as indicative of the existence of open savanna vegetation formations near to the lake. However, it would also be important to consider the size of the lake basin sampled, as a small lake basin captures a proportionally larger local pollen signal (e.g. shoreline vegetation) than a larger basin (Sugita, 1993).

Other common taxa which are likely to represent a regional pollen signal (i.e pollen derived from outside of the study site) are *Alchornea* and *Cecropia* as these are also wind-pollinated taxa (Webster, 2004; Berg, 2004c) and are well represented in evergreen forest ecosystems (Killeen and Schulenberg, 1998). However, both these taxa can also grow upon the raised termite mounds of the *pampa termitero* ecosystem so there is the possibility that these pollen types have both a regional and local source area.

Pollen of the common savanna trees *Curatella americana* and *Byrsonima* are present in both types of savanna at low abundances (maxima = 1.25% and 0.87% respectively). Pollen of the savanna shrubs, *Schleffera* and *Alibertia,* is also found in both types of savanna, although again at low percentages. *Alibertia* is absent from most pollen traps but has a maximum abundance of 6.00% in T103-01, whilst

Schleffera is present in the majority of pollen traps from both types of savanna at low percentages (<6%). The savanna herbs, Asteraceae and Cyperaceae, are present in all three sites but particularly well represented in the TO1 site (3.95% and 22.35% respectively). Other savanna herbs, such as *Borreria, Chamaesyce* and *Cuphea* have much lower abundances across the three sites (figure 5.6). *Borreria* and *Chamaesyce* occur in both types of savanna but *Cuphea* is only found within the modern pollen rain of the upland savanna site (FC1) with a mean of 0.42%.

The palms *Mauritia* and *Maurtiella* are very representative of swamps and inundated areas. The fan palm, *Mauritia flexuosa* is a dominant tree within the wet campo areas of the Cerrado Biome, where the soils are waterlogged during the wet season but experience drier conditions during the dry season (Ratter *et al.*, 1997). These species were only observed within the TO1, *pampa termitero* site, where they were often found at the margins of the raised termite mounds. However, the pollen representation of these palms is fairly low (mean = 0.92%, min = 0%, max = 6.02%) and are not present within all pollen traps from the seasonally-flooded savannas. The *Mauritia/Mauritella* taxonomic group often reach high percentages, e.g. over 80% of the pollen sum in some fossil records (Mayle *et al.,* 2000; Bush *et al.,* 2000) indicating that this may be an artefact of preferential preservation compared with other pollen grains, as both *Mauritia* and *Mauritella* have fairly large grains (~40µm) with a thick exine. These characteristics would also hinder dispersal of *Mauritia* and *Mauritella* pollen by wind. Therefore, they may not be captured effectively in pollen traps that are 0.5 m above the ground level, with the majority of the pollen falling on the ground immediately surrounding the tree and rain-wash resulting in the transportation of this pollen into a lake.

A modern pollen rain study from the cerrado of Brazil (Salgado-Labouriau, 1979) showed that other than Poaceae, the other dominant family was Fabaceae (3.2%). Another comprehensive study of the modern pollen rain of the cerrado of Brazil was by Ledru (2002), who demonstrated that the dominant herbaceous taxa, apart from Poaceae, were Asteraceae and *Borreria*, with tree and shrub pollen from *Qualea, Ilex*, Mimosoideae, *Schefflera, Caryocar* and *Byrsonima*. Of these taxa

Mimosoideae, *Schefflera* and *Byrsonima* were found within the modern pollen rain of the savanna ecosystems studied in this research, pollen of *Qualea* and *Caryocar* were not found in the samples and only one pollen grain of *Ilex* was identified.

Within NKMNP there has been a modern pollen rain study from a *cerradão* site by Gosling (2004), which reveals similar results to the *campo cerrado* site (FC1) under study in this research. The main taxa (those with a mean >3%) observed in the *cerradão* site were Moraceae/Urticaceae (25%), Poaceae (13%), *Solanum* (7%), Myrtaceae (4%), *Euterpe* (4%), *Alchornea* (4%), *Borreria* (3%) and *Cecropia* (3%). Poaceae percentages were lower in the *cerradão* site than the *campo cerrado* site (12.79 ± 2.57% (1 S.E, n = 20) vs. 29.56 ± 2.54% (1 S.E, n = 12). Note that Gosling (2004) used a pollen count size of 100 grains per pollen trap rather than the 300 used in this study). This is likely to be a result of the lower grass cover at the *cerradão* site, as the more abundant trees and shrubs of this ecosystem will create a denser canopy than that observed at the *campo cerrado* site and this will limit the development of a ground cover of grasses. Both sites have a notable Moraceae/Urticaceae signal (*campo cerrado* = 35.06 ± 2.46% (1 S.E, n = 12) and *cerradão* = 25.87 ± 1.94% (1 S.E, n = 20)) which can likely be attributed to the areas of evergreen rainforest situated within a few kilometres of these sites. *Solanum* and Myrtaceae generally have much higher abundances at the *cerradão* site and this may be attributed to pollen deposition by plants of these taxa which were in close proximity of the pollen traps causing the mean percentages to be relatively high.

5.6.2. Modern pollen rain of SDTF ecosystems

The pollen signature of the seasonally-inundated SDTF site (MV1) is dominated by *Cecropia* (figure 5.8), which is a prolific producer of small, light and well dispersed pollen grains (Bush and Riviera, 1995). *Cecropia* is the sixth most abundant plant within the vegetation plot and it appears that those traps which were located close to a *Cecropia* tree are likely to have a severe over-representation of *Cecropia* within the pollen rain. Once the *Cecropia* is removed from the pollen sum, the dominant pollen

taxon is Moraceae/Urticaceae (39.00%). Of the Moraceae family, the species, *Brosimum guianense* (% of stems = 0.57%), *Brosimum lactescens* (% of stems = 1.26%) and *Sorocea guilleminiana* (% of stems = 4.36%) are all present within the vegetation of the plot and it is assumed that some of the Moraceae/Urticaceae pollen group is of a local origin i.e from species within the plot. The presence of the genera *Pourouma* and *Maquira/Pseudolmedia* within the Moraceae/Urticaceae component of the modern pollen rain of this site (figure 5.12) shows that some of the Moraceae/Urticaceae pollen is of a regional nature as these genera are more typical of evergreen forest ecosystems (Killeen and Schlenberg, 1998) and are not found within the vegetation of this site.

The high percentage of Asteraceae pollen (mean = 6.32%) at this site is surprising as this family is often found in pollen records associated with more open vegetation formations such as savanna (Ferraz-Vicentini and Salgado-Labouriau, 1996). Within NKMNP, Asteraceae species can often occur as herbs, vines or lianas in seasonal forest assemblages (Killeen and Schulenberg, 1998) and it is assumed that the pollen is derived from these species. The pollen taxa, *Doliocarpus* and *Banisteriopsis* are also likely to be produced by lianas within the site.

Physocalymma scaberrimum is the most abundant plant within the vegetation plot and has an average pollen percentage of 4.90%. The species appears to have a wide ecological tolerance within the Neotropics as shown by its presence in several different vegetation formations. Within NKMNP it is inferred to be typical of semi-deciduous forests (Killeen, 1998) and within the Chiquitano dry forest of Bolivia it is particularly common towards the ecotone with cerrado savannas (Jardim *et al.,* 2003). It is also common in the cerrado of Brazil; Ratter *et al.* (2003), found it to be present within 49 out of 376 cerrado sites and considered it to be indicative of mesotrophic soils, such as would be found within the alluvial soils of riverine SDTF. Within Mato Grosso state of Brazil, *P. scaberrimum* is found within a range of ecosystems including gallery forests, valley forests and ecotonal areas between dry forest and *cerradão* (Ratter *et al.,* 1973; Marimon *et al.,* 2002; Pinto *et al.,* 2005), although notably it is absent from the open cerrado savanna formations of this region

(Ratter *et al.,* 1973). From present day observations of this species, it occurs within a widespread number of ecosystems and it is difficult to infer any particular habitat preference for this species.

There have only been limited floristic investigations of this seasonally-inundated SDTF formation within NKMNP (Killeen, 1998). Hence, it is difficult to infer the regional significance of this site as the current geographical extent of this vegetation formation is uncertain. However, floristically the site appears similar to a seasonally-inundated semi-deciduous forest unit described by Navarro and Maldonado (2005), which has a canopy height of 20-25 m and typical species include *Inga* spp. and *Cecropia* spp., along with a subset of the SDTF species described previously.

Of the dominant pollen taxa at the upland SDTF (CP1) site (figure 5.8), most of these taxa are representative of SDTF from the region, for example, *Acalypha* is a common shrub/herb that can grow in clearings within SDTF (Jardim *et al.,* 2003; Marchant *et al.,* 2002). *Sebastiania* is a common shrub with a number of species within the Chiquitano dry forest (Jardin *et al.,* 2003). Although it is not possible to differentiate palynolgically the Combretaceae and Melastomataceae families within NKMNP, most of the pollen from these samples is inferred to be *Combretum leprosum*, since this species is common within the vegetation plot (% of total stems = 16.98%) and is a common species within well drained and secondary SDTF sites (Jardim *et al.,* 2003). *Anadenanthera colubrina* is a key dry forest species with a widespread distribution in the Neotropics and is an indicator for the South American tropical seasonal forests phytogeographic unit which extends from north-east Brazil to south-west Bolivia and into the Andean valleys of Peru and Ecuador (Prado, 2000), indicating the wide geographical extent of this taxon in seasonal forests.

Other taxa have a more widespread neotropical distribution, e.g. *Cedrela/Trichilia* and *Piper*. *Trichilia* is a widespread genus within tropical seasonal forest and *Cedrela* can be a common emergent in Amazonian forest (Marchant *et al.,* 2002). However, the species found in the Cerro Pelao site are *Trichilia elegans* and *Cedrela*

fissilis, which are common species in the Chiquitano dry forest (Jardim *et al.,* 2003). *Piper* has a widespread distribution and has a mix of growth forms (Gentry, 1993).

The Moraceae/Urticaceae pollen at this site (figure 5.12) is likely to reflect a mix of pollen derived from plants in the SDTF at the Cerro Pelao site and additionally the evergreen rainforest ecosystems which surround this site. Within the Cerro Pelao sites, *Maclura tinctoria* (Moraceae) and *Urera caracasana* (Urticaceae) are both present in the vegetation and both could be contributing to the Moraceae/Urticaceae undifferentiated component at this site (figure 5.12). The presence of a regional Moraceae/Urticaceae component from the areas of evergreen forest that surround this site is produced by the presence of the *Brosimum* and *Maquira/Psuedolmedia* pollen within the pollen traps (figure 5.12). Trees of these genera are common within the evergreen forest ecosystems of NKMNP (Killeen and Schulenberg, 1998) but are not found within the Cerro Pelao sites so it is assumed that this reflects a pollen signal from the evergreen forest which surrounds this site.

The two surface lake sediments from the western margins of the Bolivian Pantanal (Laguna La Gaiba and Laguna Mandioré) show the dominance of Poaceae and Cyperaceae pollen which together consist of greater than 50% of the pollen sum. This signal is indicative of the permanent marshes and seasonally-inundated savanna vegetation of the Pantanal complex to which these lakes are connected. Despite being flanked by the eastern margin of the Chiquitano dry forest (figure 5.3), SDTF taxa only provide a small contribution to the pollen sum of these sites, through low percentages of *Anadenanthera, Acalypha* and *Astronium* pollen. It appears that in the sediments of these two lakes, the dry forest pollen signal is easily diluted by pollen indicative of the Pantanal vegetation complex. The large mats of aquatic grasses and sedges of the Pantanal can deposit their pollen directly into the water column so that it becomes dominant relative to pollen derived from the SDTF on upland areas where a proportion of the pollen remains in the terrestrial environment. Both lakes also have inflow from the Pantanal so high concentrations of Poaceae and Cyperacae are also likely to be transported into the lake via rivers.

Laguna Socorros is located within the SDTF of Eastern Bolivia. The pollen signal is dominated by Poaceae and Cyperaceae, probably provided by shoreline vegetation and areas of open ground surrounding the lake (figure 5.4), as these taxa only form a minor part of the limited ground cover of the SDTF surrounding the lake. SDTF elements are represented by *Gallesia* (16.99%), which is a common tree of semi-deciduous forests of the Chiquitano dry forest (Jardim *et al.,* 2003). This taxon appears to be a prolific pollen producer but is absent from SDTF ecosystems of NKMNP. Other SDTF taxa such as *Anadenanthera, Astronium* and *Acalypha* are also represented at this site.

There has only been limited previous research into the modern pollen rain of neotropical seasonally dry forests. A previous study upon a dry forest site (site code = AC2) near to NKMNP by Gosling (2004), found similar results to the Cerro Pelao site represented here. The main taxa in this site were *Anadenanthera* (27%), Moraceae/Urticaceae (22%), *Attalea* (7%), Poaceae (5%) and *Schefflera* (3%) (Gosling, 2004). The taxa at the CP1 site with a percentage >3% are Moraceae/Urticaceae (26%), *Cecropia* (11%), *Acalypha* (8%), Combretaceae/Melastomataceae (7%), *Sebastiania* (5%), *Trema* (4%), Pterophyta (3%), *Celtis* (3%). The key difference between these two sites is the abundance of *Anadenanthera* pollen which is much lower at the CP1 site (2.87 ± 0.57% (1 S.E, n = 12)) than the value observed by Gosling (2004) of 25.98 ± 5.05% (1 S.E, n =20). The reason for this is unclear as they compose a similar percentage of stems ≥10 cm dbh at both sites (AC2 = 6.94%, CP1 = 7.94%). The pollen accumulation rate of *Anadenanthera* is much greater at the AC2 site (819 grains $cm^{-2}yr^{-1}$ (Gosling, 2004)), than at the CP1 site (73 grains cm^{-2} yr^{-1}), hence the differing percentages do not appear to be an artefact of dilution of the *Anadenanthera* pollen by other pollen types at the CP1 site relative to the AC2 site. The percentage of *Attalea* pollen is also much lower at the CP1 site (0.17 ± 0.05% (1 S.E, n = 12)) than that observed at the AC2 site (7.09 ± 2.52% (1 S.E, n =20)), this may be attributed to differing vegetation between the two SDTF plots with the *Attalea* accounting for 3.66% of all stems at the AC2 plot but 0% of the stems at the CP1 site. The higher concentrations of Combretaceae/Melastomataceae and *Sebastiania* at the CP1 site relative to the AC2

site is likely to be a result of the higher abundances of these plant taxa at the CP1 site (Combretaceae/Melastomataceae = 17.46% of all stems at CP1 and 5.59% of all stems at CP1. *Sebastiania* = 3.17% of all stems at CP1 and 1.35% of all stems at AC2). The key similarity between these two sites is the presence of *Anadenanthera* pollen.

Another modern pollen rain study of seasonally dry forest in Brazil (Ledru, 2002) found the presence of Palmae, *Gallesia*, Mimosoideae, Myrtaceae, Asteraceae, Poaceae and fern spores. *Gallesia* pollen was largely absent from the dry forest plots within NKMNP. However, *Gallesia integrifolia* is found within the semi-deciduous forests of the Chiquitano dry forest of Bolivia, especially upon rich soils in riverine forests (Jardim *et al.,* 2003) and high percentages of *Gallesia* pollen (16.99%) were found within the surface sediments of Laguna Socorros from within this forest. The taxon also occurs in the lake sediments of the Western Pantanal although here the percentages are lower due to dilution by Poaceae and Cyperaceae of the Pantanal complex.

There have been very limited studies of the modern pollen rain of tropical dry forests in other areas of the Neotropics. A modern pollen rain study from tropical dry forest in Costa Rica (Rodgers III and Horn, 1996) was dominated by *Anacardium* type; other important taxa were diporate Urticales, Poaceae, *Bursera* and *Quercus*. The pollen signature is very different from that observed in this research, most likely due to the large geographical distance between the sites.

5.6.3. Pollen/vegetation relationships

Wind-pollination is very rare within the woody species of tropical ecosystems. An investigation of the pollination biology of a cerrado area in Brazil by Martins and Batalha, (2006) found that of 99 species of woody vegetation, 55.6% were mainly pollinated by bees, 20.2%, by small insects, 13.1% by moths, 5.0% by bats, 3.0% by beetles, 2.0% by hummingbirds and just 1.0%, by wind. An additional neotropical pollination study of tree species in the evergreen forests of Costa Rica (Bawa *et al.,*

1985) found just 2.5% of the species to be wind pollinated. Wind-pollination is much more common in the herbaceous stratum of neotropical ecosystems due to the prevalence of Poaceae and Cyperaceae which are usually wind-pollinated (Davis, 2004; Thomas; 2004).

Bush (1995), suggested a hierarchy by which to estimate the potential pollen representation of a plant species by investigating its reproductive/pollination mechanism. The three different hierarchies are as follows: (1) wind > small insects > bat > bee > moth > hummingbird > cleistogamy; (2) Dioecy > monoecy > hermaphroditism; (3) Allogamy > autogamy. This hierarchy will be used to explain the observed variations in pollen/vegetation ratios calculated in this research.

FC1, upland savanna

Despite Poaceae having a relative cover in this site of 51.01%, it is under-represented in the modern pollen rain with a pollen/vegetation ratio of 0.58 (table 5.10). This is despite Poaceae being wind-pollinated, an attribute that according to the Bush (1995) hierarchy should result in a high representation in the pollen rain. The reason for the low ratio of Poaceae is a result of its dilution by pollen types such as Moraceae/Urticaceae, *Cecropia* and *Alchornea,* which are taxa with hermaphrodite or monoecious flowers and are wind-pollinated. Studies have shown that these taxa are dominant within the modern pollen rain of evergreen forest ecosystems (Gosling *et al.,* 2005; Burn, 2008). The pollen accumulation rates of the evergreen rainforest ecosystems are much higher than those of savanna ecosystems. For example, for evergreen forest, Burn (2008) calculated a pollen accumulation rate of 6492 ± 3025 grains cm^{-2} yr^{-1} per year against a mean of 2789 ± 1052 grains cm^{-2} yr^{-1} per year for the FC1 savanna site (table 5.7) and it seems likely that these forest taxa are diluting the Poaceae pollen signal.

Of the major plant taxa present within this site, several of the dominant trees and shrubs are absent from the modern pollen rain e.g. *Maytenus spinosa, Lafoensia vandelliana, Eriotheca gracilipes, Bauhinia rufa, Tabebuia roseo-alba* and *Caryocar*

brasiliense. This is likely to be a result of these species being animal-pollinated and having a specialised system of pollen dispersal.

FT, seasonally-inundated savanna

This site is dominated by herbaceous and gramineous vegetation which are under-represented in the modern pollen rain of the site (p/v<1, table 5.9) e.g. Poaceae (p/v = 0.27), Cyperaceae (p/v = 0.80), Eriocaulaceae (p/v = 0.01) and Xyridaceae (p/v = 0.09). Poaceae and Cyperacae are both wind-pollinated, however, Eriocaulaceae and Xyridaceae are animal pollinated (Linder and Rudall, 2005), which could explain the much lower p/v ratio of these two families relative to Poaceae and Cyperaceae. Several of the dominant pollen types are not present within the vegetation, (e.g. Moraceae/Urticaceae and *Euterpe* type*)* and are inferred to represent a "regional" evergreen forest signal as described in the previous section.

MV1, seasonally-inundated SDTF

The three most common taxa in this vegetation plot, *Physocalymma scaberrimum, Hirtella gracilipes* and *Inga ingoides* are all under-represented (p/v ratio <1) in the modern pollen rain of the site with modern pollen/vegetation ratios of 0.36, 0.07 and 0.01 respectively. These three taxa all have hermaphrodite flowers and are animal-pollinated (Bush, 1995, Graham, 2004). According to the above hierarchy, these attributes are liable to result in under-representation in the pollen rain. Other dominant taxa in the vegetation plot are completely absent from the modern pollen rain of the ecosystem, e.g. *Xylopia sericea, Bauhinia rufa, Qualea cordata, Tapirira guianensis, Nectandra acutifolia, Lacistema aggregatum, Cariniana domestica* and *Ceiba samauma*. According to the Bush hierarchy it is assumed that these taxa would be insect-pollinated and have hermaphroditic flowers. However, some of these taxa can have unisexual flowers e.g. Lacistemataceae, Lauraceae and *Tapirira (*Bush, 1995; Daly, 2004; Madriñan, 2004).

The taxa that are over-represented (p/v ratio >1) are *Cecropia* and Moraceae/Urticaceae. These taxa are wind-pollinated and produce large amounts of small light pollen designed to be dispersed effectively by wind. *Cecropia* was extremely over-represented within this site, it is the sixth most abundant taxon in the vegetation plot in terms of number of stems and is known to be a prolific pollen producer (Bush and Riveria, 1995). There are also several pollen types that occur in the modern pollen rain of the ecosystem without being present in the vegetation, e.g. Asteraceae, *Celtis*, Poaceae, Cyperaceae, *Schefflera* and *Acalypha* (table 5.10). The majority of these taxa occur as plants with a dbh of less than 10 cm (i.e. as herbs and shrubs), hence will not have been included within the vegetation surveys despite their likely presence in the sub canopy/ground cover of this ecosystem, e.g. Asteraceae, Poaceae, Cyperaceae, *Schefflera* and *Acalypha*. Several of these taxa are also wind-pollinated, so are liable to be over-represented within the modern pollen rain, e.g. *Celtis,* Poaceae and Cyperaceae.

CP1, upland SDTF

Of the major taxa in the vegetation of this site, some are completely absent from the modern pollen rain of the site, e.g. *Aspidosperma cylindrocarpon, Aspidosperma macrocarpon, Callisthene fasciculata, Bauhinia rufa, Amburana cearensis, Pseudobombax longiflorum.* These taxa all have hermaphrodite flowers which is liable to result in under-representation in the modern pollen (Bush, 1995). Only one taxon present in both the vegetation and the modern pollen rain has a positive pollen/vegetation ratio, namely *Sebastiania* (p/v ratio = 1.45). *Sebastiania* is monoecious and is pollinated by small insects (Bush, 1995) and these two attributes are likely to result in a reasonable representation of *Sebastiania* within the pollen rain according to the Bush (1995) hierarchy. However, the distribution of this taxon within the pollen traps of the site is highly variable. From observation of the data it appears that one of the traps (T65) has high *Sebastiania* percentages during each year of sampling; hence it may be inferred that the close proximity of the trap to an individual of *Sebastiania* may have caused the high local deposition and the high pollen/vegetation ratio observed.

There are also several pollen taxa with a mean percentage of greater than 3% which were not listed within the vegetation surveys (e.g. *Celtis,* Pterophyta, *Trema, Acalypha* and *Cecropia*). *Cecropia, Celtis*, and *Trema* are anemophilous and are widespread in a number of different vegetation formations across the NKMNP from evergreen forest to more seasonal forests (Killeen and Schulenberg, 1998). Hence their presence within the pollen traps is likely to represent a regional pollen signal. *Acalypha* is typically a herb and will not have been inventoried in the vegetation survey as it is likely to have a dbh<10 cm as will any Pterophyta. Both these taxa are common in SDTF ecosystems so it is likely that pollen from these taxa is of a more local nature.

5.6.4. Pollen accumulation rates

The pollen accumulation rates for the three savanna sites (table 5.7) range from 2237 grains cm^{-2} yr^{-1} to 3330 grains cm^{-2} yr^{-1} and these values are similar to those estimated from a *cerradão* savanna within NKMNP of approximately 2000 grains cm^{-2} yr^{-1} (Gosling *et al.,* in press). The SDTF ecosystems from within NKMNP have pollen accumulation rates of 1689 grains cm^{-2} yr^{-1} (excluding *Cecropia* pollen) for the seasonally-inundated SDTF site and 2435 grains cm^{-2} yr^{-1} for the upland SDTF site (table 5.7). These values are lower than those calculated for a different SDTF site close to NKMNP of approximately 4000 grains cm^{-2} yr^{-1} (Gosling *et al.,* in press). The variation in pollen accumulation rates between the different ecosystems will be discussed in chapter 6.

5.6.5. Inter-annual variability

The modern pollen rain of the ecosystems studied is observed to vary on an annual basis (Hicks, 1999; Fontana, 2003) and several taxa show notably variable profiles during the three years of sampling (figures 5.6 to 5.9). For example, within the seasonally-inundated savanna (TO1) site, Cyperaceae and Poaceae both show annual variability. Cyperaceae has an annual minimum of 13.10% during the 2000 sampling year and a maximum of 28.11% during the 2001 sampling year. Poaceae has an annual minimum of 9.18% during the 1999 sampling season and a maximum

of 35.74% during the 2000 samping season. Within the upland savanna site (FC1), *Borreria* type 1, has an annual minimum of 0.34% during the 1999 sampling season and a value of 5.33% during the 2001 sampling season. Within the upland SDTF site (CP1), the pollen type, unknown type df 61, has a maximum of 21.02% during the 2000 sampling season and a value of just 0.58% during the 1999 sampling season. The annual pollen accumulation rates at each ecosystem also show a degree of variability (table 5.7).

Studies from Northern Europe have proposed that pollen production can be correlated with climatic parameters (Hicks, 1999; Sjogren *et al.,* 2006). In a study of artificial pollen traps from other ecosystems to those studied in this research from NKMNP, Gosling *et al.* (2005) suggested that the pollen traps from the year 1999 had lower pollen accumulation rates than the 2000 and 2001 samples and that this was attributable to lower precipitation during the 1999 sampling year. This pattern is not observed for the ecosystems studied in this research. It is proposed that a longer sampling period than three years is required to test the relationship between pollen productivity and climatic parameters for neotropical environments.

As the pollen spectra obtained from lake sediments are a composite of several years of pollen accumulation, this research emphasises the importance of sampling the modern pollen rain of an ecosystem over a period of several years. This will ensure that the pollen spectrum of a single year's sample is not unrepresentative of the ecosystem when compared to the average modern pollen rain produced on a longer timescale.

5.6.6. Intra-site variability

Several artificial pollen traps were analysed for each year of sampling from each site and this allows the intra-site variability within the modern pollen rain to be observed (figures 5.6 to 5.9). Pollen traps are expected to show variability within each site in response to different plant species surrounding them at each sampling point and there is some evidence of the pollen traps being biased by vegetation in close proximity to

them. For example, Asteraceae pollen is highly variable within the 1999 samples from the seasonally-inundated savanna site (TO1), with a maximum of 28.33% and a minimum of 1.00%. It is evident here that one of the traps has been biased by the close proximity of a plant of the Asteraceae family.

Several taxa at the upland savanna (FC1) and seasonally-inundated savanna (FT) sites also show spatial variability (figure 5.6). For example, within the FC1 site, *Borreria* type 1 has a maximum of 18% and a minimum of 0% for the samples from 2001, some pollen traps are liable to be much closer to plants of *Borreria* type 1, hence capture a greater abundance of its pollen type. In the FT site, Pterophyta – trilete has a very variable profile with a value of 20.60% in trap T122-99 yet was absent from the next trap (T123-99), which is 50m further along the transect. Again this emphasises the influence of the local vegetational heterogeneity upon the pollen composition of artificial pollen traps.

Within the upland SDTF (CP1) site the mean abundance of *Sebastiania* pollen of 4.60% is largely driven by a high percentage within three traps from the same location over the three years (T65), this implies that this pollen trap was likely to be located in very close proximity to a *Sebastiania* plant. Other pollen traps along the transect contain no pollen grains of *Sebastiania* e.g. T67-99, T68-99, implying that the pollen of this taxon is not well dispersed in this site. *Phyllanthus acuminatus* shows a similar pattern with annual maxima being recorded in the trap at location T62 over the three years, implying that this trap was located in close proximity to a plant of this species. Interestingly, only one other pollen grain of this taxon was found at another trap location at this site (T68-00), implying that pollen of *Phyllanthus acuminatus* is very poorly dispersed.

Within the seasonally-inundated SDTF plot, several taxa show evidence of spatial variability, for example, *Cecropia* has an extremely variable profile across the site with a maximum percentage of over 2000% of the pollen sum and a minimum of 3.01% of the pollen sum (*Cecropia* was excluded from the pollen sum – see section 5.5.4). The pollen type, unknown df 61, also shows variation in abundance along the

transect of pollen traps. It has a value of 4.52% at trap T31-00 at the start of the transect, 14.95% at trap T35-00 and 43.61% at trap T39-00 at the end of the transect. This variability is likely to result from a plant of this taxon being very close to some of the pollen traps, hence these traps capturing much pollen of this taxon. Other taxa that show notable spatial variability at this site are *Doliocarpus,* Asteraceae, unknown df 58 and unknown df 80 (figure 5.8).

The high degree of intra-site variability observed within the pollen traps discussed above and observed in figures 5.6 to 5.9, shows that it is important to ensure that multiple pollen traps are taken from the ecosystems to ensure that a representative pollen signal is captured. As the artificial pollen traps are known to capture a local pollen signal relative to lake sediments, by averaging the modern pollen rain of 12 pollen traps from three years of sampling, it is assumed that any artefacts of local over-representation of certain pollen taxa within the pollen traps are minimised. This means that any differences between the modern pollen rain of an ecosystem due to the different sampling techniques (artificial pollen traps vs. lake sediments) are minimised.

5.6.7. Comparison between pollen signals from artificial pollen traps and surface lake sediments.

The results from figure 5.13 show that all the surface lake sediment samples plot together as a cluster in the centre of the diagram, separated by the savanna pollen trap samples to the left and the SDTF pollen traps samples to the right. This indicates the importance of sampling environment and geographic location upon the modern pollen rain spectra obtained, which seems to outweigh the variation in ecosystem pollen signatures observed within these samples. This is likely to be due to certain taxa being dominant within each sampling environment. Analysis of the pollen diagrams for these sites shows the dominance of Poaceae and Cyperaceae within the surface lake sediments and the dominance of Moraceae/Urticaceae within the artificial pollen traps from NKMNP. A modern pollen rain study from various ecosystems within Canada also showed that samples tended to separate on the basis

of sampling environment (moss cushions and lake sediments) rather than by ecosystem (Birks and Birks, 1980).

Due to difficulty of analysing the similarities between the two sampling environments by the cluster analysis (figure 5.13), it was decided to visually interpret the pollen spectra to investigate the key similarities between the pollen traps and surface lake sediments (figures 5.6 to 5.11). The seasonally-inundated savanna lake and pollen trap samples are both dominated by the savanna taxa Poaceae, Cyperaceae and Asteraceae, with Moraceae/Urticaceae and *Cecropia* representing a regional pollen signal of evergreen forest within the regions of sampling. Visual analysis of the pollen diagrams from the SDTF samples shows that the representative pollen taxa of SDTF in both the pollen traps and surface lake sediments are Moraceae/Urticaceae, *Acalypha, Astronium* spp. and *Anadenanthera,* although these are at lower abundances in the lake sediments due to their dilution by Poaceae and Cyperaceae pollen of an aquatic and regional nature.

Several taxa observed at fairly high abundances within the artificial pollen traps are present at only very low percentages/absent within the surface lake sediments, for example, *Sebastiania* (maximum mean = 4.60% in pollen traps from site CP1, and maximum mean in SDTF lakes = 1.00%) and *Phyllanthus acuminatus* (maximum mean = 1.43% in pollen traps from site CP1 and absent from SDTF lake sediments). Savanna trees, shrubs and herbs (e.g. *Borreria, Byrsonima, Curatella americana* and *Cuphea*) occur at much higher percentages within the savanna artificial pollen traps than the savanna surface lake sediments. This is due to the pollen traps capturing a local pollen signal of the vegetation immediately surrounding them. These taxa are also all animal pollinated (see section 6.6.3) and the pollen would therefore be expected to be poorly dispersed in the air. Within the lake sediments these taxa will be diluted due to the lake capturing pollen from numerous different ecosystems and the biasing of the pollen spectra in favour of those with good dispersal properties (e.g. wind-pollinated taxa).

5.7. Summary of chapter

This chapter describes the modern pollen rain of the savanna and SDFT sites. The results show that the upland savanna is dominated by pollen of Moraceae/Urticaceae (35.1%), Poaceae (29.6%), *Alchornea* (6.1%) and *Cecropia* (4.1%), whilst the seasonally-inundated savanna sites are dominated by Moraceae/Urticaceae (30.7%), Poaceae (19.5%), Cyperaceae (14.0%) and *Cecropia* (7.9%). The main taxa in the modern pollen rain of the upland SDTF are Moraceae/Urticaceae (25.8%), *Cecropia* (10.5%), *Acalypha* (7.6%) and Combretaceae/Melastomataceae (6.7%). Seasonally-inundated SDTF is dominated by *Cecropia* pollen to the extent that it was removed from the pollen sum and the main non-*Cecropia* pollen types are Moraceae/Urticaceae (39.0%), unknown type df 61 (6.4%), Asteraceae (6.3%), *Celtis* (6.0%) and *Physocalymma scaberrimum* (4.9%). The modern pollen rain obtained from the surface lake samples is generally complementary to that obtained from the artificial pollen traps for a given ecosystem in terms of the key taxa present.

Analysis of the artificial pollen traps from NKMNP shows that the modern pollen rain of these ecosystems exhibits both intra-site and inter-annual variation in response to pollen traps being biased by the surrounding vegetation and differential pollen production of plants on annual timescales. Modern pollen/vegetation ratios show that many key vegetation types are absent/under-represented within the modern pollen rain

The following chapter will use the modern pollen rain data described in this chapter to investigate the extent to which these ecosystems can be palynologically differentiated. Multivariate statistics will be used to test the separation of upland and seasonally-inundated savannas and to identify the taxa responsible for any palynologically differences between these two ecosystems. The same test will then try to identify any palynologically differences between the upland and seasonally-inundated SDTF ecosystems. The results of this will have important implications for the reconstruction of vegetation assemblages from fossil pollen records.

Chapter 6. Differentiation of neotropical savannas and seasonally dry tropical forests by their modern pollen rain

Contents

6.1. Introduction to chapter *155*

6.2. Statistical analysis *155*

6.3. Results *157*

6.3.1. Summary pollen diagram 157

6.3.2. Palynological differentiation of savanna ecosystems at NKMNP 157

6.3.3. Palynological differentiation of SDTF ecosystems at NKMNP 157

6.3.4. Palynological differentiation of seasonally-inundated savanna and SDTF ecosystems from surface lake sediments 158

6.3.5. Palynological differentiation of savanna and SDTF ecosystems within NKMNP 158

6.3.6 Statistical differences in pollen accumulation rates between ecosystems 159

6.4. Discussion *167*

6.4.1. Differentiation of savanna ecosystems 167

6.4.2. Differentiation of SDTF ecosystems 173

6.4.3. Differentiation of savanna and SDTF ecosystems 175

6.5. Summary of chapter *181*

6.1. Introduction to chapter

The aim of this chapter is to determine the degree to which different savanna and seasonally dry tropical forest ecosystems (SDTF) can be differentiated by their modern pollen rain. This aim is tested using visual comparison of the pollen diagrams and ordination methods of the modern pollen rain data described in chapter five. Four different ordinations are performed. The first ordination contains only the savanna pollen trap data and tests the degree to which upland savannas and seasonally-inundated savannas can be differentiated palynogically. The second ordination contains only the SDTF data and tests the degree to which upland SDTF and seasonally-inundated SDTF can be differentiated palynologically. The third ordination uses the modern pollen data obtained from the surface lake sediments and tests the degree to which the samples from lakes within seasonally-inundated savannas can be differentiated from those from within SDTF ecosystems. The final ordination combines the pollen trap data from the savanna and SDTF ecosystems studied in this research with data from a previous study of artificial pollen traps from different SDTF and savanna sites within Noel Kempff Mercado National Park, Bolivia by Gosling (2004). The implications of these results for the interpretation of fossil pollen records are then discussed.

6.2. Statistical analysis

To investigate the palynological differences between the different ecosystems, visual comparison of pollen diagrams and ordination methods were used. The pollen diagram plotted includes the average pollen rain of a site for the artificial pollen traps and the average modern pollen rain within the surface sediment of a lake. Ordination is a multivariate data analysis technique that aims to present different sites in a two-dimensional space so that sites with a high degree of taxonomic similarity plot close to each other, whilst those sites with a high degree of taxonomic dissimilarity plot far apart from each other (ter Braak, 1995). Principal component analysis (PCA) was selected as the ordination technique due to criteria outlined in ter Braak (1995),

which suggests the initial application of an ordination technique that reflects a unimodal response model, such as Detrended Correspondence Analysis (DCA) to investigate the gradient lengths within the data. If these are less than about two standard deviations then it is recommended that an ordination technique that encompasses a linear response model (such as PCA) is more appropriate. As the initial ordinations displayed low gradient lengths of approximately two standard deviations, PCA was selected as the appropriate ordination method for the data.

Prior to the ordination, the data were square-root transformed as recommended for percentage data (Birks, 1986; Prentice, 1986). This is to reduce the variance within the dataset, therefore reducing the influence of dominant taxa. The ordinations were performed using the C2 version 1.5 software package (Juggins, 2003) and the Community Ecology Package version 1.8-5 (Oksanen *et al.,* 2007) available as freeware in R (R Development Core Team, 2007).

The first ordination contains the modern pollen rain data derived from the savanna pollen traps and the second ordination contains the modern pollen rain data derived from the SDTF pollen traps from NKMNP. For these ordinations each sample was the pollen count percentage data from one artificial pollen trap. *Cecropia* pollen was removed from the second ordination due to it being excluded from the pollen sum of the seasonally-inundated SDTF site (see section 5.5.4). The third ordination contains the pollen percentages from the surface lake sediments and each sample is the percentage pollen data from one surface sediment sample. The final ordination contains modern pollen rain data from savanna and SDTF ecosystems within NKMNP. This ordination combines the modern pollen rain data from the five ecosystems analysed by the author with data from another two ecosystems analysed by Gosling (2004). As the sample set of individual pollen trap data was much larger for this ordination (n = 100), to simplify the interpretation of the diagram the annual average pollen rain of each site was calculated and this dataset (n=20) was used for the ordination.

To test the differences in PARs between the different ecosystems, the non-parametric Kruskal-Wallis test was selected, as the data showed non-normal distributions (Fowler *et al.,* 1998). Prior to the analysis, *Cecropia* pollen was removed from the PARs of all sites for consistency, as it was removed from the pollen sum of the MV1 site (see section 5.5.4). This allowed the PARs to be comparable between sites. The test was performed using SigmaPlot version 11 (Systat Software, 2008).

6.3. Results

6.3.1. Summary pollen diagram

The summary pollen diagram is shown in figure 6.1.

6.3.2. Palynological differentiation of savanna ecosystems at NKMNP (figure 6.2)

The first two axes explain 36.52% of the variance (λ_1 = 26.72%, λ_2 = 9.80%). The ordination diagram shows a slight separation of the two savanna ecosystems, with the upland savannas tending to plot towards the negative end of PCA axis 1 and the seasonally-inundated savanna samples plotting towards the positive end of PCA axis 1. However, there is a degree of overlap between the two ecosystems. The key taxa (those with the highest magnitude taxon scores on PCA axes 1 and 2) are shown in table 6.1 and the remaining taxon scores and eigenvectors are presented in the appendix.

6.3.3. Palynological differentiation of SDTF ecosystems at NKMNP (figure 6.3)

The first two axes explain 39.40% of the variance (λ_1 = 29.50%, λ_2 = 9.90%). The key taxa (those with the highest magnitude taxon scores on PCA axes 1 and 2) are shown in table 6.2 and the remaining taxon scores and eigenvectors are presented in the appendix. The ordination diagrams show a good separation between the seasonally-inundated and upland SDTF plots, with seasonally-inundated SDTF sites plotting on the positive end of axis 1 and upland SDTF sites plotting on the negative

end of axis 1. The taxa which are representative of the upland SDTF (with the taxon scores in brackets) are *Acalypha* (-4.40), *Sebastiania* (-2.90), Pterophyta - trilete (-2.51), *Piper* (-2.46) and *Cedrela/Trichilia* (-2.25). The key taxa that are representative of the inundated SDTF are unknown type df 61 (3.96), *Physocalymma scaberrimum* (3.96), Asteraceae (3.32), *Doliocarpus* (1.99) and *Simarouba* (1.45).

6.3.4. Palynological differentiation of seasonally-inundated savanna and SDTF ecosystems from surface lake sediments (figure 6.4)

The first two axes explain 47.96% of the variance (λ_1 = 33.47%, λ_2 = 14.49%). The key taxa (those with the highest magnitude taxon scores on PCA axes 1 and 2) are shown in table 6.3 and the remaining taxon scores and eigenvectors are presented in the appendix. The ordination diagram shows a good separation between the samples from the seasonally-inundated savannas of the Beni Basin and the samples from within SDTF ecosystems. The taxa which are representative of the seasonally-inundated savanna (those with negative taxon scores on PCA axis one) are Cyperaceae (-4.57), Asteraceae (-3.90), Pterophyta – trilete (-2.68), Polypodiaceae – verrucate (-1.87) and Polypodiaceae – psilate (-1.64). The key taxa that are representative of the lakes from SDTF (those with positive taxon scores on PCA axis 1) are Poaceae (4.00), *Anadenanthera* (2.48), *Acalypha* (2.31), *Trema* (1.66) and unknown type df 88 (1.60).

6.3.5. Palynological differentiation of savanna and SDTF ecosystems within NKMNP (figure 6.5)

The first two axes explain 43.30% of the variance (λ_1 = 25.92%, λ_2 = 17.38%). The key taxa (those with the highest magnitude taxon scores on PCA axes 1 and 2) are shown in table 6.4 and the remaining taxa scores and eigenvectors are presented in the appendix. Axis 1 of the ordination diagrams shows a good separation between the samples from the SDTF ecosystems and those from savanna ecosystems. The main taxa which are representative of the SDTF pollen traps are *Anadenanthera* (9.79), *Acalypha* (3.61), *Piper* (3.38), *Attalea* (3.27) and Pterophyta – trilete (3.27), whilst those which are representative of the savanna sites at NKMNP are Poaceae (-

9.06), Cyperaceae (-7.69), *Alchornea* (-4.44), *Borreria* type 1 (-2.31) and Moraceae/Urticaceae (-2.29).

6.3.6. Statistical differences in pollen accumulation rates between sites

The results of the Kruskal-Wallis test showed that the differences between the pollen accumulation rates of the five different sites were not significant ($H = 8.381$ with four degrees of freedom, $P = 0.079$, therefore $P > 0.05$).

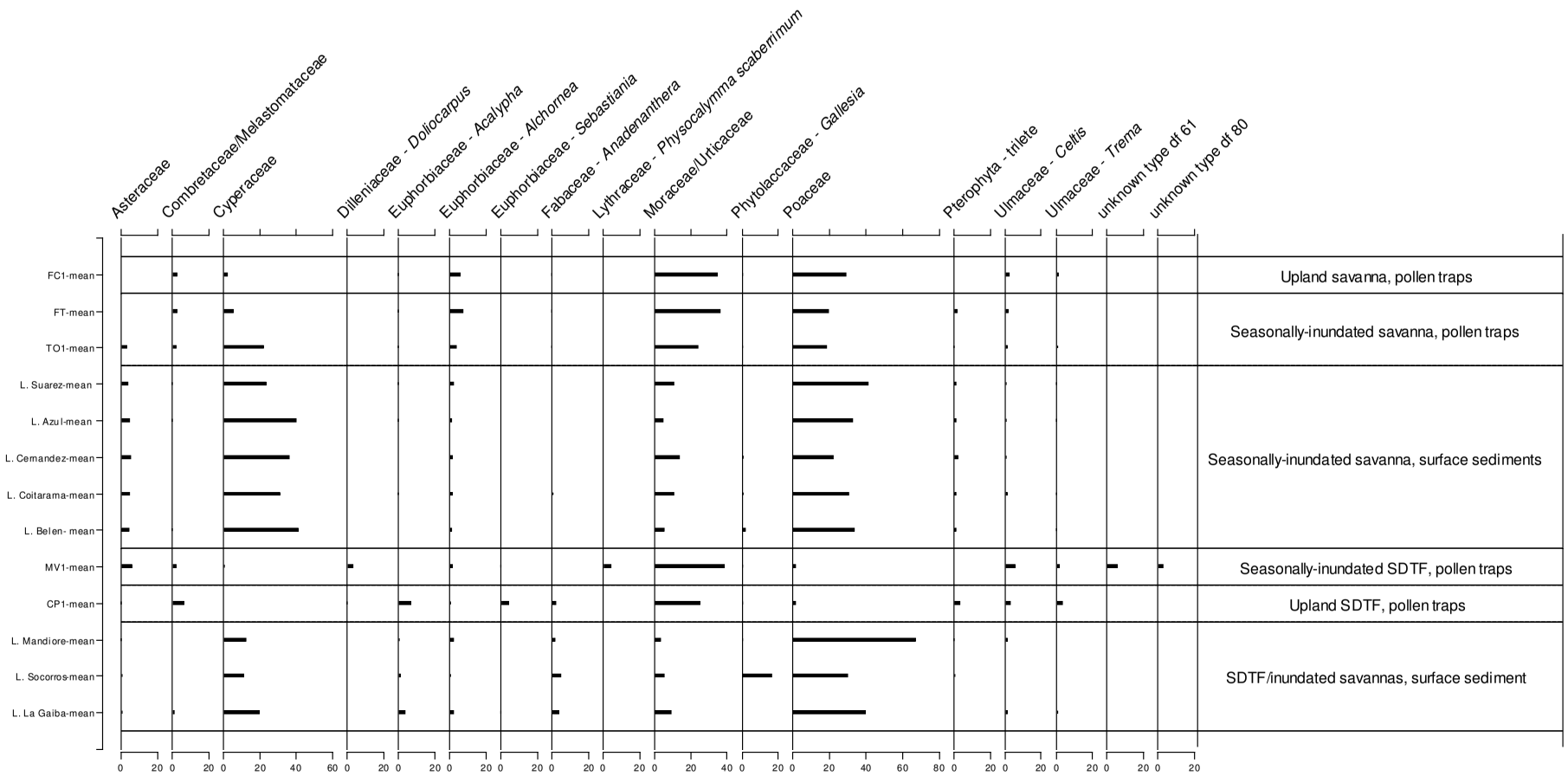

Figure 6.1. Summary pollen percentage diagram, showing all taxa with a minimum abundance of ≥3% in any one sample. Note that *Cecropia* is not included in the diagram as it was excluded from the pollen sum of some samples due to severe over-representation in the modern pollen rain.

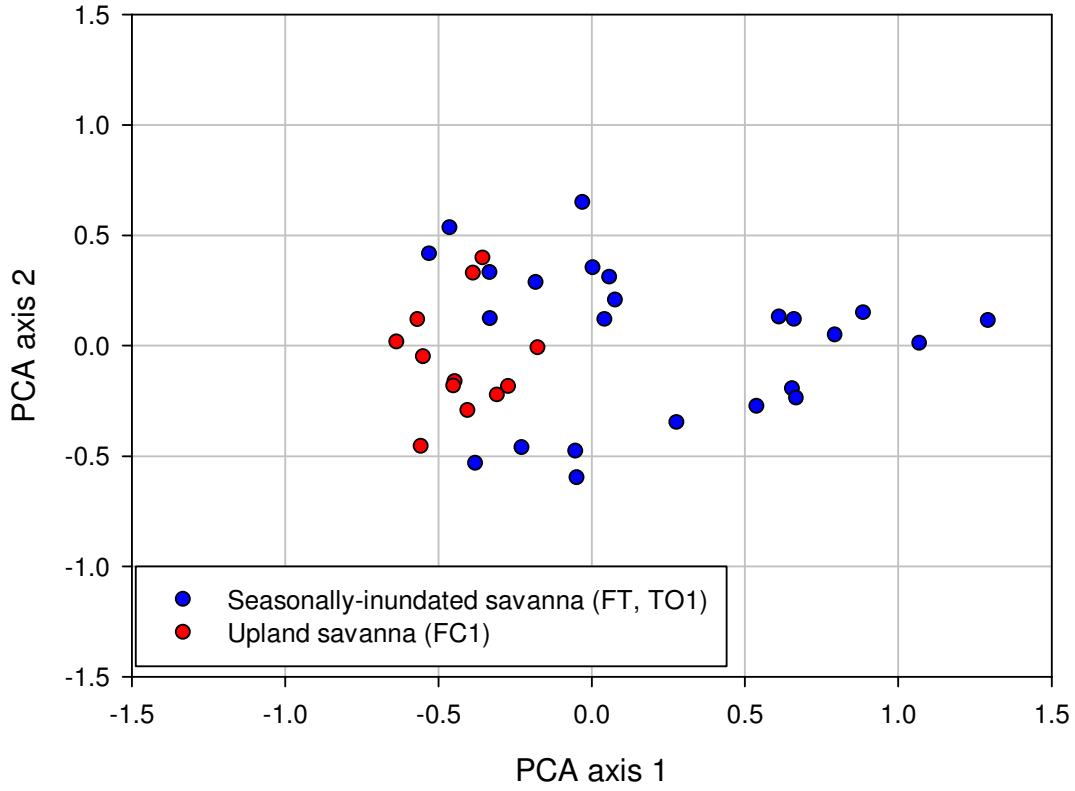

Figure 6.2. PCA site plot of savanna modern pollen rain samples derived from artificial pollen traps from NKMNP, Bolivia. Each point on the graph represents the pollen count of one pollen trap (approximately 300 pollen grains).

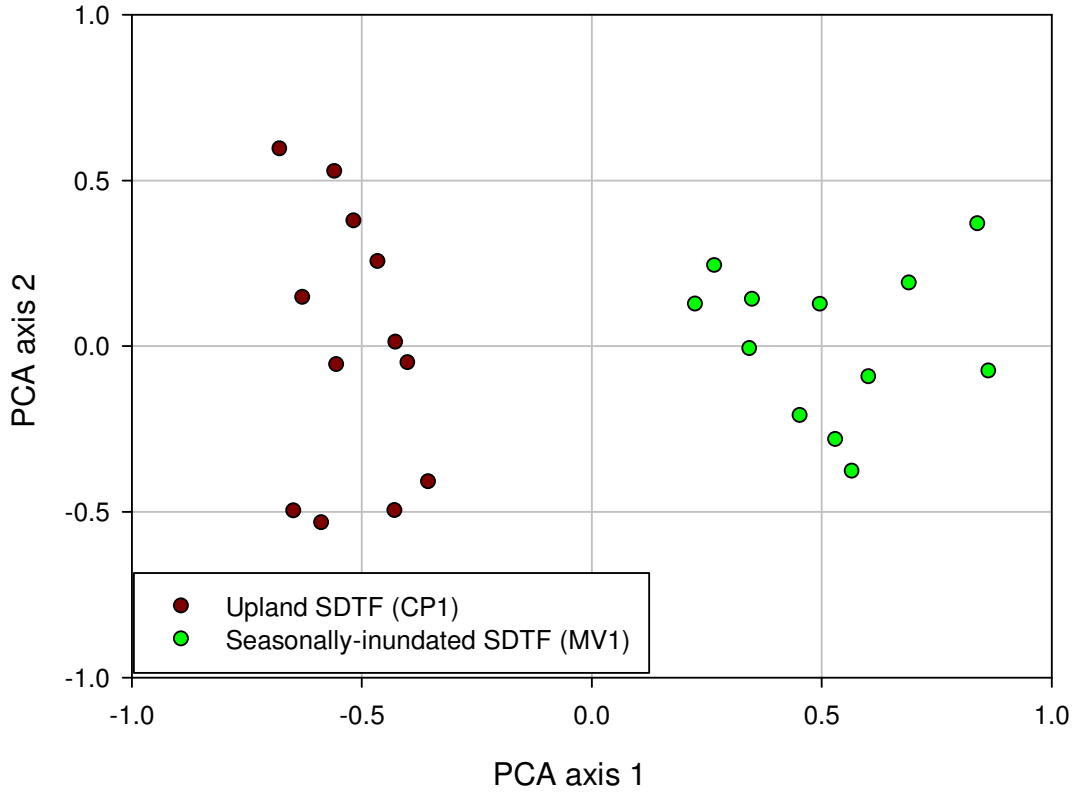

Figure 6.3. PCA site plot of SDTF modern pollen rain samples derived from artificial pollen traps from NKMNP, Bolivia. Each point on the graph represents the pollen count of one pollen trap (approximately 300 pollen grains).

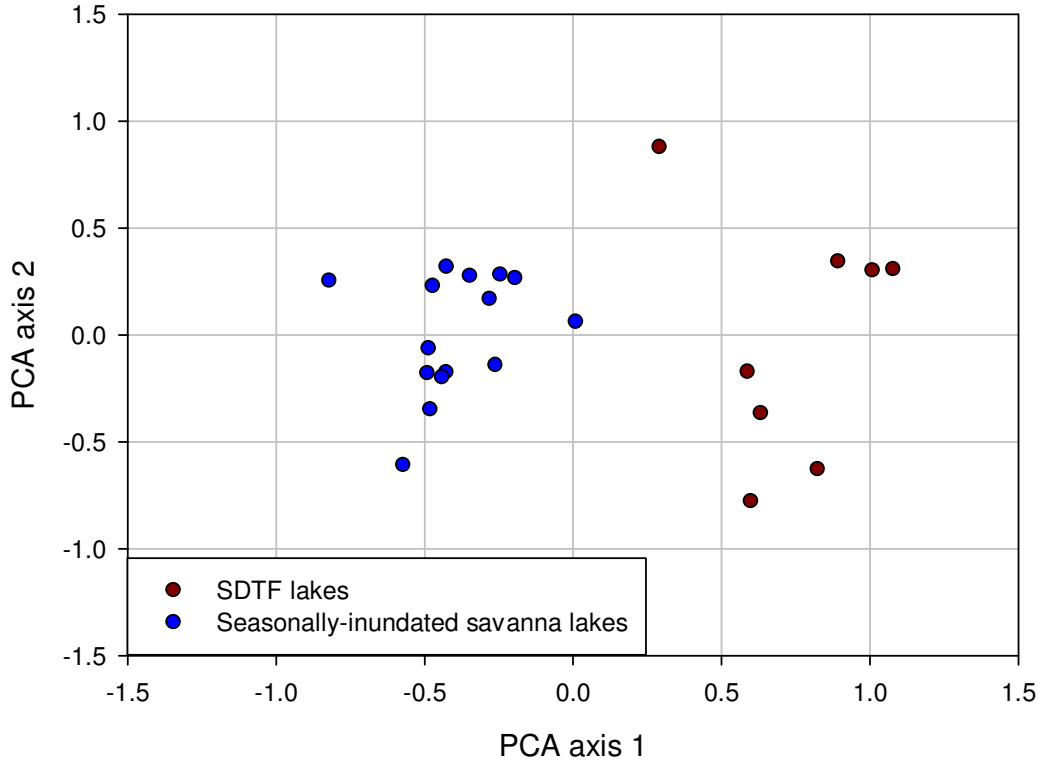

Figure 6.4. PCA site plot of modern pollen rain samples of SDTF and seasonally-inundated savanna ecosystems derived from surface lake sediments from across lowland Bolivia. Each point on the graph represents the pollen count of one surface sediment sample (approximately 300 pollen grains).

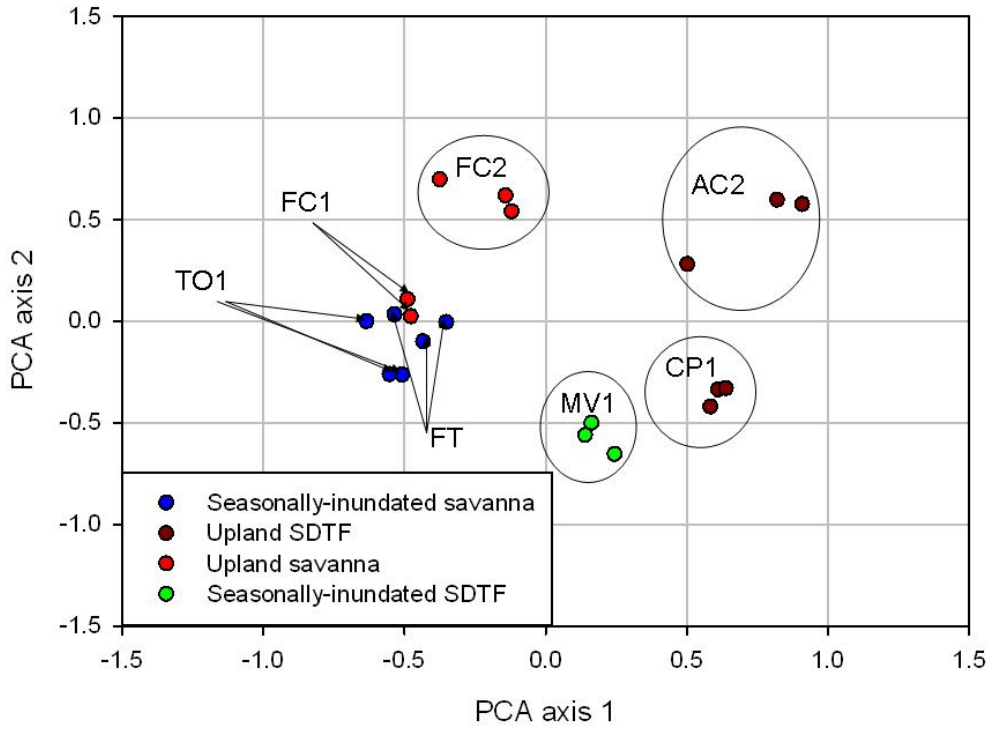

Figure 6.5. PCA site plot of samples of modern pollen rain of SDTF ecosystems and savanna ecosystems derived from artificial pollen traps from within NKMNP, Bolivia. TO1 = seasonally-inundated savanna, FT = seasonally-inundated savanna, FC1 = upland savanna (*campo cerrado),* FC2 = upland savanna *(cerradão*), MV1 = seasonally-inundated SDTF, CP1 = upland SDTF, AC2 = upland SDTF. Each point on the graph represents the average annual pollen count of the site (minimum pollen count = 500 grains).

Taxon	Taxon score on PCA axis 1	Taxon	Taxon score on PCA axis 2
Cyperaceae	9.27	Moraceae/Urticaceae	5.25
Asteraceae	4.41	Pterophyta - trilete	3.55
Cecropia	3.84	*Schleffera*	3.23
Chamaesyce	1.39	*Euterpe* type	3.09
Borreria type 2	1.29	*Curatella*	2.73
Alchornea	-1.50	*Cecropia*	-1.52
Euterpe type	-1.62	*Mauritia/Mauritiella*	-1.99
Borreria type 1	-1.68	Cyperaceae	-2.07
Moraceae/Urticaceae	-3.23	*Borreria* type 1	-2.08
Poaceae	-6.16	Poaceae	-8.89

Table 6.1. The key taxa (those with the highest magnitude taxon scores) on PCA axis 1 and PCA axis 2 for the ordination of the modern pollen rain from savanna ecosystems derived from artificial pollen traps (figure 6.2).

Taxon	Taxon score on PCA axis 1	Taxon	Taxon score on PCA axis 2
Unknown type df 61	3.96	*Sebastiania*	5.41
Physocalymma scaberrimum	3.96	*Acalypha*	2.93
Asteraceae	3.32	Unknown type df 61	2.77
Doliocarpus	1.99	*Cedrela/Trichilia*	2.37
Simarouba	1.45	Moraceae/Urticaceae	2.26
Cedrela/Trichilia	-2.25	*Inga*	-2.86
Piper	-2.46	*Serjania*	-2.92
Pterophyta - trilete	-2.51	Unknown type df 40	-3.07
Sebastiania	-2.90	Pterophyta - trilete	-3.23
Acalypha	-4.40	Asteraceae	-3.49

Table 6.2. The key taxa (those with the highest magnitude taxon scores) on PCA axis 1 and PCA axis 2 for the ordination of modern pollen rain from SDTF ecosystems derived from artificial pollen traps (figure 6.3).

Taxon	Taxon score on PCA axis 1	Taxon	Taxon score on PCA axis 2
Poaceae	4.00	*Gallesia*	5.32
Anadenanthera	2.48	Unknown type df 88	2.34
Acalypha	2.31	Poaceae	2.20
Trema	1.66	Pterophyta - trilete	1.15
Unknown type df 88	1.60	Unknown type 103	1.12
Polypodiaceae - psilate	-1.64	*Dalbergia/Machaerium* type	-2.43
Polypodiaceae - verrucate	-1.87	Palmae - Undiff	-2.46
Pterophyta - trilete	-2.68	Fabaceae - Mimosoideae undiff	-2.47
Asteraceae	-3.90	Moraceae/Urticaceae	-2.96
Cyperaceae	-4.57	*Cecropia*	-3.18

Table 6.3. The key taxa (those with the highest magnitude taxon scores) on PCA axis 1 and PCA axis 2 for the ordination of the modern pollen rain of seasonally-inundated savannas and SDTF ecosystems derived from surface lake sediments (figure 6.4).

Taxon	Taxon score on PCA axis 1	Taxon	Taxon score on PCA axis 2
Anadenanthera	9.79	Poaceae	5.25
Acalypha	3.61	*Anadenanthera*	4.71
Piper	3.38	*Borreria* type 1	4.08
Attalea	3.27	*Solanum*	3.96
Pterophyta - trilete	3.27	*Euterpe* type	3.75
Moraceae/Urticaceae	-2.29	Moraceae/Urticaceae	-3.88
*Borreri*a type 1	-2.31	*Physocalymma scaberrimum*	-3.93
Alchornea	-4.44	*Celtis*	-4.10
Cyperaceae	-7.69	Unknown type df 61	-4.31
Poaceae	-9.06	Cyperaceae	-5.20

Table 6.4. The key taxa (those with the highest magnitude taxon scores) on PCA axis 1 and PCA axis 2 for the ordination of the modern pollen rain of SDTF ecosystems and savanna ecosystems derived from artificial pollen traps from within NKMNP, Bolivia (figure 6.5).

6.4. Discussion

6.4.1. Differentiation of savanna ecosystems

The ordination diagram (figure 6.2) shows a slight separation of the two different types of savanna (upland and seasonally-inundated) but there is also a degree of overlap between samples from the two ecosystems. The seasonally-inundated savanna samples tend to have higher percentages of Cyperaceae and Asteraceae, and lower percentages of Poaceae relative to the upland savanna samples. The pollen accumulation rates for the two different savanna types are also very similar (see table 5.7).

Observation of the pollen data (see appendix) shows that some more minor pollen taxa may have importance in separating these two types of savanna. *Mauritia/Mauritella* pollen is primarily found within the TO1 seasonally-inundated savanna site. Only one grain of this taxon was found in the FC1 upland savana site and it has a strong positive taxon score of 1.09 on PCA axis 1 of the ordination, therefore indicative of seasonally-inundated savanna sites. The palms *Mauritia* and *Mauritella* tend to be found in wet campo areas of the Cerrado Biome where soils are waterlogged in the wet season (Ratter *et al.,* 1997), hence are representative of seasonally-inundated ecosystems. The two morphological types of *Borreria* observed in the pollen data are also representative of different sites. The polyporate type (*Borreria* type 1) has a negative taxon score of -1.68, therefore is representative of the upland savanna ecosystems, whilst the zonocolpate type (*Borreria* type 2) has a positive taxon score of 1.29, therefore is representative of the seasonally-inundated savannas. It was not possible to identify these two types to species level so it is difficult to confirm whether these *Borreria* types have different ecological requirements.

This slight separation of the two savanna types by their modern pollen rain is contrary to the strong separation of these savannas on the basis of the floristic data (see chapter 4). The reason for this discrepancy appears to be the limited

palynological taxonomic resolution of key savanna taxa found within the pollen traps (e.g. Poaceae, Cyperacae and Asteraceae) and that several key taxa which drive the separation at the floristic level are absent or have very low abundance in the modern pollen rain of these ecosystems. The plant families that were found to be more common in the seasonally-inundated savannas in NKMNP (according to their taxon scores described in chapter 4) are Poaceae, Sterculiaceae, Cyperaceae, Lamiaceae and Xyridaceae. Of these families the highest Poaceae percentages actually occur in the upland savanna site (FC1). Sterculiaceae is absent from the modern pollen rain of all the savanna sites. Greater Cyperaceae percentages do occur in the seasonally-inundated sites, agreeing with the data obtained from chapter 4. Lamiaceae and Xyridaceae occur in the pollen rain of the seasonally-inundated savanna sites although at very low abundances. Lamiaceae is represented by *Hyptis* pollen, with two grains in the TO1 site and ten grains in the FT site, whilst it is absent from the FC1 upland savanna site. Xyridaceae pollen was only found within one trap from the FT site where it was represented by six pollen grains, it is absent from the other two savanna sites. Therefore, although their abundance is very low, these two pollen taxa do show some ecological preference for seasonally-inundated savannas.

The plant taxa that are indicative of upland savannas in NKMNP (according to their taxon scores described in chapter 4) are Clusiaceae, Proteaceae, Fabaceae, Bombacaceae and Erythroxylaceae. Clusiaceae is represented in the FC1 upland savanna site by just two pollen grain of *Kielmeyera.* Proteaceae is represented in the modern pollen rain of the savanna ecosystems by *Roupala*. However, this pollen type is indistinguishable from pollen of the liana, *Paulinia* (Sapindaceae) and the pollen type is found in all three savanna sites at very low abundances (FC1 = 0.17%, FT = 0.03%, TO1 = 0.33%). Bombacaceae pollen is absent from the modern pollen rain of all three savanna sites. Fabaceae pollen is found at low abundances across all savanna sites (FC1 = 1.20%, FT = 0.75%, TO1 = 0.75%). However, it is very difficult to identify pollen of this family to the generic level and as Fabaceae is very common in other ecosystems in NKMNP it is difficult to infer the extent to which this represents a regional pollen signal derived from outside the study plot. Erythroxylaceae is absent from the modern pollen rain of the two seasonally

inundated savanna sites and it is represented in the upland savanna site by just one pollen grain of *Erythoxylum*. Therefore, the indicative plant taxa are extremely poorly represented within the modern pollen rain of the upland savanna site.

Implications for fossil pollen records - savanna indicator taxa

There are many potential pollen indicator taxa for savanna ecosystems that have been suggested in the literature. The following section will investigate the potential of these with consideration of the results from this research.

Brosimum gaudichaudii (Moraceae)

Burn and Mayle (2008) assert that *Brosimum gaudichaudii* has potential as a savanna indicator due to its ecological preference for savanna habitats within NKMNP and its distinct pollen morphology. However, subsequent scans of several savanna samples revealed that none of the Moraceae/Urticaceae pollen observed could be attributed to this taxon, despite its presence in the vegetation of the FC1, *campo cerrado* site with a relative cover of 0.93%. This finding was somewhat surprising as *B. gaudichaudii* is a wind-pollinated species (Martins and Batalha, 2006) and would be expected to produce relatively high quantities of pollen. Numerous pollen grains of other *Brosimum* spp. from areas of evergreen rainforest were found within the savanna pollen traps (figure 5.12). The reason for the absence of *B. gaudichaudii* from the pollen traps is unclear. It may be a low pollen producer relative to the other *Brosimum* spp. living in evergreen forest species due to the physiological stresses in the savanna caused by a severe soil water-deficit in the dry season relative to areas of evergreen forest. Additionally, as it is commonly a shrub in savanna ecosystems, it has a much smaller stature than *Brosimum* spp. found in evergreen forests, therefore its flowering will be much less profuse and this could result in a low contribution to the modern pollen rain.

Byrsonima (Malpighiaceae)

Byrsonima crassifolia is a common botanical indicator of savannas across the Neotropics (Furley, 1999) and *Byrsonima* spp. are common within the savanna ecosystems of NKMNP (Killeen and Schulenberg, 1998). *Byrsonima* has been cited as a good savanna pollen indicator that is over-represented in the modern pollen rain by Ledru (2002) from cerrado areas in central Brazil. Although several studies have resolved this taxon to generic level identification (e.g. Ferraz-Vicentini and Salgado-Labouriau, 1996; Behling and Hooghiemstra, 2000; Ledru *et al.,* 2006), some have also combined it with *Dalbergia* (Fabaceae) and *Machaerium* (Fabaceae) due to morphological similarities (e.g. Gosling *et al.,* 2005; Burbridge *et al.,* 2004). Within this study a *Byrsonima* type was identified and a *Dalbergia/Machaerium* type was identified. It is worth noting that species of *Machaerium* and *Dalbergia* were absent from the vegetation of all savanna sites studied in NKMNP and this could explain the very low percentages of this pollen type in the savanna traps. The *Byrsonima* pollen type was also seldom observed, with the mean percentage at all savanna sites being <1%, so although it has applicability as a savanna indicator taxon, it only occurs at very low levels within both types of savannas in NKMNP.

Curatella americana (Dilleniaceae)

Ecologically, *Curatella americana*, is restricted to savanna habitats (Killeen and Schulenberg, 1998) and is a commonly adopted cerrado indicator (Furley, 1999). It is not represented within most pollen traps, however, it has locally high abundances within some traps (maximum = 7.89% in T109-99), indicating that the pollen of *Curatella americana* may be poorly dispersed. The pollination mechanism is entomophilous with bee pollination observed for this taxon (Ramirez, 2004).

Mayle *et al.* (2000) asserted that the Early and Mid-Holocene section of cores from Laguna Bella Vista and Laguna Chaplin within NKMNP reflected expansive seasonally-inundated savannas due to the presence of pollen of Poaceae and *Curatella americana.* In this study, the tree *Curatella americana* is found within both

the upland savanna sites and upon termite mounds within the seasonally-inundated savanna ecosystems, although it does seem to have an ecological preference for growing upon termite mounds in the seasonally-inundated savanna sites (see chapter 4). The pollen of *Curatella americana* was also found within both upland and seasonally-inundated savannas at similar percentages, (TO1 = 0.43%, FC1 = 1.25%, FT = 1.00%), hence it is difficult to ascertain using these results whether the savanna signal within the Holocene section of these cores reflects upland or seasonally-flooded savannas.

Schefflera, formerly *Didymopanax* (Araliaceae)

This taxon has been termed a savanna indicator taxa by several authors (Behling and Hooghiemsta, 2000; Ledru, 2002). It is animal-pollinated and the pollinators are small insects (Martins and Batalha, 2006). Within the samples, *Schefflera* is a common taxon in both types of savanna at low percentages (TO1 = 1.03%, FT = 2.28%, FC1 = 1.30%) and it seems that a considerable amount of pollen must be liberated to the atmosphere during pollination to result in the relatively abundant deposition of its pollen in the pollen traps. Over-representation of *Schefflera* pollen was also observed by Gosling *et al.* (in press), who attributed it to the very open flower structure and its exposed anthers. Although some species of *Schefflera* are common within savanna ecosystems of South America, it is very difficult to differentiate these species by their pollen morphology from other species which are representative of other vegetation formations. The *Schefflera* pollen type is commonly found within other vegetation formations (e.g. evergreen rainforest and seasonally dry tropical forest (Gosling *et al.,* in press; Burn, 2008 and this research) indicating that the taxon is a habitat generalist and it cannot be used as a savanna indicator without full consideration of the entire pollen spectra.

Caryocar (Caryocaraceae) and *Stryphnodendron* (Fabaceae)

Although both these taxa are suggested by Colinvaux *et al.* (1999) to be useful as savanna indicators, none of their pollen was found within the pollen traps. This is

despite both *Caryocar brasiliense* and *Stryphnodendron guianense* being present in the savannas of NKMNP (Killeen and Schulenberg, 1998). *Caryocar* was also found to be under-represented in the modern pollen rain of a cerrado ecosystem in Central Brazil by Ledru (2002). *C. brasilienses* has large pollen (55µm x 45µm) and is animal-pollinated with the main pollinators being bats and moths (Gribel and Hay, 1993). *Stryphnodendron* is also animal-pollinated (Martins and Batalha, 2006). These attributes are likely to result in poor representation in the modern pollen rain.

Herbaceous taxa - Borreria (Rubiaceae)*, Cuphea* (Lythraceae), *Hyptis* (Lamiaceae), Xyridaceae

Borreria species are common savanna herbs. Two morphological types of *Borreria* pollen were found within the pollen traps; a polyporate type occurred within the *campo cerrado* site, whilst a zonocolpate type predominated within the seasonally-inundated savanna sites. *Cuphea* spp. can be common herbs within savannas but other species can exist within forest settings (Killeen and Schulenberg, 1998) and observations show very low pollen abundance across all savanna sites (TO1 = 0%, FT = 0%, FC1 = 0.42%). As *Cuphea* can only be differentiated to genus level, the habitat preference of the genus means that *Cuphea* cannot be used as a savanna indicator without consideration of the full pollen spectrum. Analysis of the minor taxa of the savanna sites showed that *Hyptis* (TO1 = 0.06%, FT = 0.28%) and Xyridaceae (FT = 0.16%) only appear in the pollen profile of the seasonally-inundated savanna and not the upland savanna site in NKMNP, although they both occurs at very low abundance. These taxa are also very poorly represented in the modern pollen rain of the seasonally-inundated savannas of the Beni Basin. *Borreria, Cuphea* and Xyridaceae are absent and *Hyptis* is represented by just one pollen grain. In palaeoecological records, it is difficult to infer whether these taxa represent savanna vegetation or just a fringe of herbaceous vegetation growing on the seasonal margins of a lake which is otherwise surrounded by forest.

6.4.2. Differentiation of SDTF ecosystems

A good separation between the upland SDTF and seasonally-inundated SDTF is observed in the pollen diagram and the ordination (figures 6.1 and 6.3). It is clear that there are several taxa that are much more common in one type of SDTF than the other. For example, *Sebastiana, Cedrela/Trichilia, Phyllanthus acuminatus, Anadenanthera, Astronium* spp., *Acalypha* and *Selaginella* are much more common in the upland SDTF site than the seasonally-inundated SDFT site. Whilst, Asteraceae, *Doliocarpus, Physocalymma scaberrimum, Banisteriopsis* and several unknown pollen types are much more common in the seasonally-inundated SDTF site than the upland SDTF site. The taxa that are important in differentiating these two ecosystems floristically are also found within the modern pollen rain of this site (see chapter 4). For example, the pollen and plant taxa that are representative of the upland SDTF sites are *Sebastiania, Cedrela/Trichilia, Anadenanthera* and Combretaceae/Melastomataceae, whilst those representative of the seasonally-inundated SDTF site are *Physocalymma scaberrimum* and *Hirtella.*

The pollen accumulation rates for the two types of SDTF are similar once the *Cecropia* is removed from the sum for both sites (Upland SDTF = 2146 ± 1446, seasonally-inundated SDTF = 1689 ± 1035). Therefore, it is difficult to use pollen accumulation rates as well as percentage abundances as a method to differentiate between these sites.

The distinction in percentage abundances between the two types of SDTF allows an inference to be made over whether a SDTF signal from fossil pollen records is representative of local seasonally-inundated SDTF ecosystems or more regional upland SDTF ecosystems. This is important as recognition of upland SDTF in fossil pollen records would allow a regional reconstruction of the vegetation as upland SDTF would be found on the areas between the main watercourses and away from the seasonally-inundated lake margins. This will allow a detailed palaeoclimatic inference as the regional vegetation type is known. Recognition of seasonally-inundated SDTF in fossil pollen records would be indicative of a more "local" vegetation signal, for example, the vegetation upon the seasonally-inundated lake

margins or upon floodplains of the rivers that flow into the lakes. Hence, it would be difficult to make any interpretations about the type of vegetation growing upon the upland areas between the main watercourses and so any palaeoclimatic inferences from the data would be difficult as the regional vegetation formation would be unknown.

The results from the upland SDTF plot (CP1) show the presence of *Anadenanthera* which is a key taxon of the Chiquitano dry forest (Killeen *et al.,* 2006). This taxon was also found to be very abundant (27%) in the modern pollen rain of another upland SDTF plot from NE Bolivia (Gosling *et al.,* in press) and these results confirm its applicability as a pollen type associated with upland SDTF ecosystems in the region. *Anadenanthera colubrina* is one of the key indicator taxa of the "Pleistocene Dry Forest Arc" formation of seasonally forests, which is inferred to have previously covered a vast area of the southern Neotropics (Prado and Gibbs, 1993). If the presence of this taxon is found within lake sediments from areas inferred to be within this vegetation formation, it may give detail about the former extent of this vegetation formation and test the feasibility of the "Pleistocene Dry Forest Arc" theory.

Interestingly, *Anadenanthera* is only found in very low abundances in the modern pollen rain of the seasonally-inundated SDTF site and is also absent from the vegetation of this site. There are two species of *Anadenanthera* (ILDIS, 2008; TROPICOS, 2008), *A. colubrina* and *A. peregrina,* but unfortunately, it is not possible to differentiate these two species palynologically. However, it appears that both species have similar ecological preferences for well-drained, upland soils. Furley and Ratter (1988) name *Anadenanthera* spp. as an indicator taxon for mesotrophic *cerradão* in Brazil*,* which is a vegetation formation that only grows upon well-drained soils. *A. peregrina* also occurs in the semi-deciduous Atlantic forests of Brazil and research has also shown a preference for this species for better-drained soils (Ferreria-Junior *et al.,* 2006). A survey of the flora of different sites in the Chiquitano dry forest of Bolivia by Killeen *et al.* (1998), shows that *A. colubrina* has a preference for the upland sites. Navarro and Maldonado, 2005 also infer that

Anadenanthera macrocarpon (a synonym of *A. colubrina*) is an element of well-drained SDTF ecosystems. These findings suggest that *Anadenanthera* spp. may only be suitable as an indicator pollen taxon for the upland variants of SDTF.

Fossil pollen records from NKMNP (Mayle *et al.,* 2000; Burbridge *et al.,* 2004) show the presence of *Anadenanthera, Astronium fraxinifolium* and *Astronium urundeuva* during the Holocene. These taxa are interpreted to represent areas of SDTF on upland non-flooded areas that surround the site and they are found within the modern pollen spectra of upland SDTF from this research, yet largely absent from the modern pollen spectra of seasonally-inundated SDTF. Therefore, the results in this research agree with the author's interpretation of the existence of SDTF on upland areas in the region at this time.

6.4.3. Differentiation of savanna and SDTF ecosystems

Lake sediments

The results show a good separation of the lakes from the two different ecosystems, with those lakes within seasonally-inundated savanna having negative values on PCA axis 1 and those within seasonally dry tropical forest ecosystems having positive values on PCA axis 1 (figure 6.4, table 6.3). The pollen taxa which are indicative of the SDTF sites are *Anadenanthera, Acalypha*, Combretaceae/Melastomataceae and *Astronium.* All these taxa are floristically representative of the Chiquitano dry forest of Bolivia (see chapter 4). *Anadenanthera* spp. and *Astronium* spp. are particularly important taxa within SDTF formations across the Neotropics (Prado, 2000). The pollen taxa which are representative of the seasonally-inundated savannas of the Beni Basin are Asteraceae, Pterophyta spores and *Mimosa*, along with taxa from the gallery forests of the region such as Moraceae/Urticaceae. Interestingly, Poaceae has a positive taxon score on PCA axis 1, implying that it is more representative of the SDTF lakes. However, the high Poaceae percentages within Laguna Mandioré and Laguna La

Gaiba is likely a regional signal as these lakes are hydrologically connected to the seasonally-inundated savannas and swamp environments of the Pantanal complex.

Artificial pollen traps

Axis 1 of the ordination diagram (figure 6.5) shows a good separation of the savanna and SDTF ecosystems within NKMNP, showing that these two vegetation types can be differentiated by their modern pollen rain. The result shown here indicates that it is possible to recognise these ecosystems in fossil pollen records. The key pollen taxa which are representative of SDTF from the ordination (those with positive taxon scores) are all well represented within the Chiquitano dry forest (Jardim *et al.,* 2003), for example, *Anadenanthera, Attalea, Acalypha, Piper* and *Sebastiania.* The key pollen taxa which are representative of savannas from this region are Poaceae, Cyperaceae, *Curatella* and *Borreria* type 1, which are all common plants found within the savannas of NKMNP (Killeen and Schulenberg, 1998). According to the ordination, Moraceae/Urticaceae and *Alchornea* are also representative of the savanna sites at NKMNP, however, it is inferred that these taxa represent a regional evergreen forest pollen signal (see section 5.6.1) as both taxa are much more common in evergreen forest ecosystems than savannas (Killeen and Schulenberg, 1998).

Moraceae/Urticaceae and *Alchornea* are wind-pollinated taxa (Berg, 2004a; Berg, 2004b; Webster, 2004) so the pollen is easily dispersed into neighbouring ecosystems (e.g. savanna or SDTF). These pollen taxa are found in all the ecosystems sampled within NKMNP. It seems that the open nature of the savannas at NKMNP, which have very limited tree canopy development, allows the pollen traps to capture a larger proportion of these pollen taxa than those traps in SDTF ecosystems. The greater tree canopy development of SDTF ecosystems will restrict the fall-out and capture of the regional evergreen forest pollen signal within the pollen traps.

Of the savanna ecosystems at NKMNP, the two seasonally-inundated savannas (TO1 and FT) and the upland *campo cerrado* savanna (FC1) sites plot very close together in the ordination, whilst the upland *cerradão* site (FC2) plots separately in the top-left quadrant. The key pollen taxa that drive the separation of the *cerradão* site from the other savanna sites are the high percentages of *Solanum* (7%) and *Borreria* type 1 (5%). However, both these plant taxa are present in various other ecosystems within NKMNP (Killeen and Schulenberg, 1998) so it appears that neither of these pollen taxa are diagnostic of the *cerradão* ecosystem.

The three SDTF sites at NKMNP also plot as three clusters (figure 6.5). The AC2 site has a negative value on PCA axis 2 whilst the CP1 and MV1 sites have positive values on the axis. The key pollen taxa that separate the AC2 site samples from the other SDTF samples are the high percentages of *Anadenanthera* (mean = 27%) and *Attalea* (mean = 7%) relative to the other two SDTF sites.

The pollen accumulation rates of the savanna and SDTF sites are similar (table 5.7 and section 6.4.6) and this finding is different to that observed by Gosling *et al,* (in press), who found that PARs were greater in a SDTF site (approximately 4000 grains cm^{-2} yr^{-1}) than an upland savanna (*cerradão*) site (approximately 2000 grains cm^{-2} yr^{-1}). *Cecropia* pollen was very low within the SDTF of Gosling *et al.* (in press), therefore it assumed that the difference is not due to including *Cecropia* pollen within the pollen sum. The SDTF and savanna sites observed by Gosling *et al.* (in press) have some floristic differences to those studied in this research and this may explain the differing findings.

Implications for fossil pollen records

A fossil pollen record from the Bolivian Pantanal has been interpreted to show regional vegetation change over the past 42000 years. A summary pollen diagram of this profile is displayed in figure 6.6 (B. Whitney, unpublished data). This record will now be interpreted with relation to the results of the modern pollen rain studies of savanna and SDTF ecosystems discussed in chapter 5.

The oldest sediments in the pollen diagram (zone 4) have been interpreted to represent an open savanna landscape (B. Whitney, *pers.com*) and the profile is dominated by Poaceae, Asteraceae, *Borreria/Spermacoce* and *Alternanthera*. With the exception of *Alternanthera,* these taxa are all abundant within the modern pollen rain studies from savanna habitats in NKNMP and the Beni Basin (see section 5.5). *Alternanthera* is commonly present on seasonally-inundated lake margins (Marchant *et al.,* 2002) and the very high percentages of *Alternanthera* (>40% in some samples of zone 4) contrasts with the values obtained from modern pollen rain studies of surface lake sediment from within the seasonally-inundated savannas of the Beni Basin, where the maximum percentage was 1.44% (Laguna Azul, figure 5.10). This implies that the surface area of the lake during this time was possibly much smaller than those lakes in the Beni Basin, as the smaller the lake basin the greater the proportion of "local" pollen (i.e. of shoreline vegetation) relative to that of "regional" pollen (Sugita, 1993).

Although the Poaceae percentages in this zone are lower than the values suggested by Bush (2002) as being strongly suggestive of savanna (50-90%), they are generally in accordance with the values observed from modern pollen rain studies of savanna ecosystems from NKMNP and the Beni Basin in this research (<50%). The pollen assemblage of zone 4 lacks the pollen of many woody vegetation types, such as *Curatella americana* and *Byrsonima,* that are present in the savanna modern pollen rain spectra of this research. This implies that the savanna ecosystems surrounding Laguna La Gaiba at this time were much more open than the physiognomies of the savannas studied in this research.

The modern pollen rain of the savanna sites in NKMNP and the Beni Basin has a regional forest signal of the wind-pollinated taxa, *Cecropia,* Moraceae/Urticaceae and *Alchornea (*section 5.5). These taxa are scarcely represented within the pollen profile at Laguna La Gaiba, implying that there was little development of evergreen forest vegetation at a regional scale.

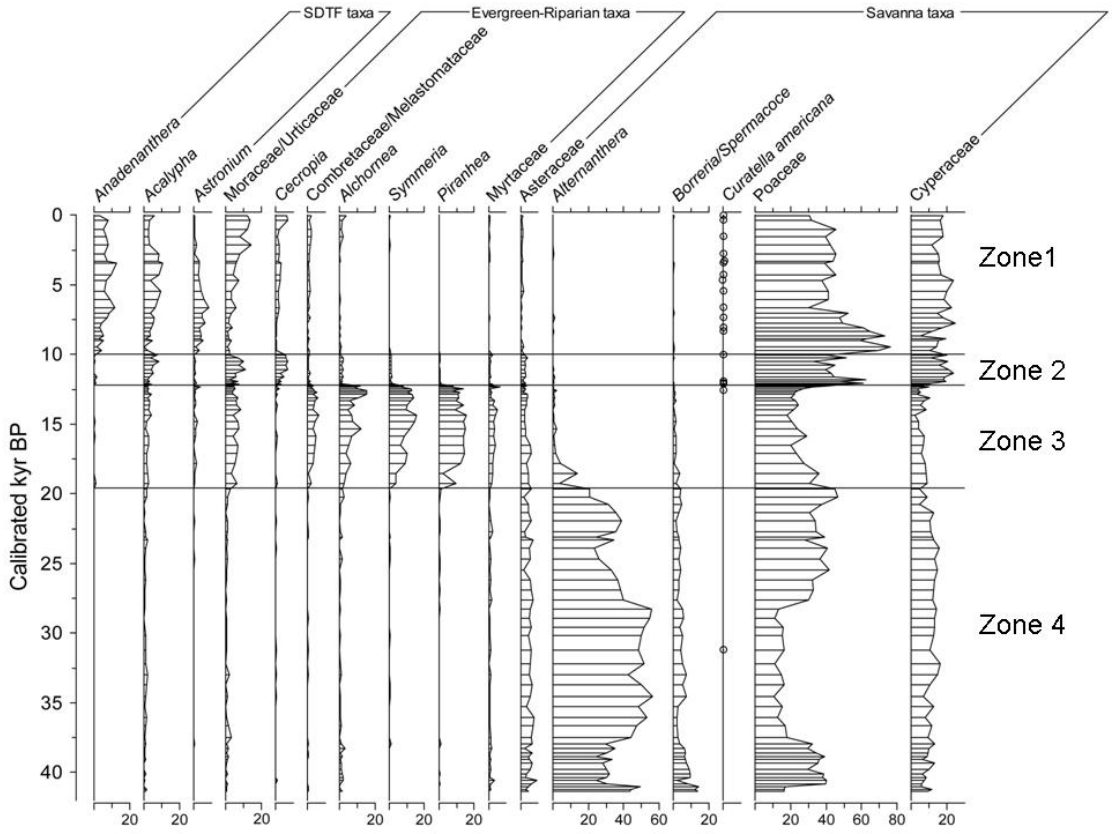

Figure 6.6. Summary pollen diagram of Laguna La Gaiba (B. Whitney, unpublished data).

Zone 3 has been interpreted to represent a riverine forest assemblage developing within the lake basin (B. Whitney, *pers. com*) which is taxonomically unlike any ecosystem studied in this research.

Zone 2 has been interpreted to represent the initial development of forest on the hills that surround the lake basin (B. Whitney, *pers. com*). Some taxa that are commonly found within the modern pollen rain of savanna ecosystems in this research, such as Asteraceae and *Borreria/Spermacoce*, decline to negligible abundance within this zone. Therefore, it appears that the forest component is expanding and reducing the diffusion of light to the ground flora, leading to the expulsion of many of the herbaceous vegetation types. The vegetation type of zone 2, represented predominantly by Moraceae/Urticaceae, *Acalypha* and *Cecropia,* is difficult to define.

Zone 1 has been interpreted to show the development of SDTF on upland areas surrounding the lake (B. Whitney, *pers. com*). The key taxa are *Anadenanthera, Acalypha* and *Astronium*. These are all taxa that are well represented in the modern pollen rain of the upland SDTF site at NKMNP (CP1, figure 5.8) and are present within the modern pollen spectra of the two other lakes from with SDTF ecosystems (Laguna Mandioré and Laguna Socorros, figure 5.10). The pollen spectra from Laguna La Gaiba lack the abundance of many of the other taxa which are present within the modern pollen rain of upland SDTF at NKMNP e.g. Combretaceae/Melastomaceae, *Cedrela/Trichilia, Sebastiania* and *Selaginella.* This could be due to floristic differences between the SDTF of these two regions.

The SDTF profile in this section is very different to the modern pollen rain spectrum of seasonally-inundated SDTF obtained from this research (figure 5.8). For example, pollen grains of Moraceae/Urticaceae, *Cecropia* and *Physocalymma scaberrimum* are of low abundance or absent from the pollen profile, therefore, it is apparent that this SDTF signal represents an upland SDTF formation that is growing upon raised areas around the lakes, rather than representing development of SDTF in seasonally-inundated areas. Additionally, the presence of *Anadenanthera* pollen at a percentage of 3-13% is much more similar to its percentage in the modern pollen rain of upland SDTF (3%), than seasonally-inundated SDTF (<1%) (figure 5.8).

Poaceae pollen is also greater in the zones 1 and 2 than zones 3 and 4. This has been interpreted to represent hydrological connection of the lake to the seasonally-flooded savannas and swamp ecosystems of the Pantanal complex (B. Whitney, *pers. com).* These seasonally-flooded savannas can be interpreted to be tree savannas similar to those observed in NKMNP due to the presence of the savanna tree, *Curatella americana.*

The modern pollen rain data from this research can be shown to improve and strengthen the interpretations of vegetation change from this lake basin. The modern analogues of savanna and SDTF have been shown to aid the identification of the

specific type of SDTF that developed around the lake basin during the Holocene and aid the recognition of savanna pollen signals within the lake.

6.5. Summary of chapter

This chapter tests the degree to which different savanna and SDTF ecosystems can be differentiated by their modern pollen rain. The results show that there is only a slight palynological separation between the upland and seasonally-inundated savanna ecosystems, this primarily being the result of higher Cyperaceae percentages in the pollen traps from seasonally-inundated savanna ecosystems. However, a good palynological separation is observed between the upland and seasonally-inundated SDTF ecosystems, meaning that these two ecosystems have the potential to be identified within fossil pollen records. The results emphasise the difficulty of differentiating savanna ecosystems in fossil pollen records, whilst palynological differentiation of SDTF ecosystems will allow much more detailed regional vegetation reconstructions to be made and hence improve palaeoclimatic inferences from fossil pollen records. A comparison is made between the floristic separation of the ecosystems observed in chapter 4 and the palynologically separation investigated in this chapter. This shows that for the savanna ecosystems, several plant taxa which are responsible for the floristic separation of these ecosystems are absent or very under-represented in the modern pollen rain. For the SDTF, the plant taxa that are responsible for the separation of these ecosystems are also found in the modern pollen rain of these ecosystems allowing them to be differentiated palynologically.

The implications of the results for fossil pollen records are discussed. Potential savanna indicator taxa and interpretations of relevant fossil pollen records from the region are discussed using the findings of this research.

The following chapter concludes this research by summarising the key results and implications for neotropical palaeoecology. It then offers a critical analysis of the methodology and suggests possible directions for future research.

Chapter 7. Conclusions

Contents

7.1. Introduction to chapter 183

7.2. Key findings of this research..... 183

7.3. Critical analysis of the methodology 185

7.4. Possible future research..... 188

7.1. Introduction to chapter

This chapter will summarise the results and implications of this research. This will be followed by a critical analysis of the sampling methodology and consideration of possible future research.

7.2. Key findings of this research

This study aimed to characterise and differentiate different savanna and seasonally dry tropical forest ecosystems (upland savanna, seasonally-inundated savanna, upland SDTF and seasonally-inundated SDTF) by their modern pollen rain. Chapter 4 shows that these ecosystems can be differentiated floristically and presents the key taxonomic groups that are responsible for this separation. Chapter 5 then presents the pollen signatures of these ecosystems. The main pollen types recorded at each site are shown in table 7.1. Chapter 6 tests the degree to which these ecosystems can be differentiated by their modern pollen rain. The results show that the two savanna ecosystems are well separated by their floristic inventories, yet only show a slight separation at palynological level. This is due to the plant taxa that control the separation at the floristic level being very poorly represented within the modern pollen rain of the savanna ecosystems. Therefore, it is also very important to consider the rare pollen taxa within the fossil pollen spectra to identify any taxa that may be representative of either type of savanna. The two types of SDTF ecosystems are well separated at both the floristic and palynological level because the plant taxa that control the separation at the floristic level are well represented within the modern pollen rain of these ecosystems, meaning that these ecosystems can be characterised and differentiated in fossil pollen records. The study of modern pollen/vegetation ratios shows that there are numerous key plant taxa from within the vegetation plots that are absent from the modern pollen rain of the ecosystem and identifies those taxa which are under-represented or over-represented within the

Site	**TO1**	**FC1**	**FT**	**CP1**	**MV1**
Ecosystem	**Seasonally-inundated savanna**	**Upland savanna**	**Seasonally-inundated savanna**	**Upland SDTF**	**Seasonally-inundated SDTF**
Dominant pollen taxa	Moraceae/ Urticaceae (24.69%)	Moraceae/ Urticaceae (35.06%)	Moraceae/ Urticaceae (36.72%)	Moraceae/ Urticaceae (25.84%)	*Cecropia* (excluded from pollen sum)
	Cyperaceae (22.35%)	Poaceae (29.56%)	Poaceae (20.10%)	*Cecropia (10.49%)*	Moraceae/ Urticaceae (39.00%)
	Poaceae (18.81%)	*Alchornea* (6.12%)	*Alchornea* (7.66%)	*Acalypha (7.61%)*	unknown type df 61 (6.41%)
	Cecropia (8.70%)	*Cecropia* (4.13%)	*Cecropia* (7.03%)	Combretaceae/ Melastomataceae (6.66	Asteraceae (6.32%)
	Alchornea (4.03%)	*Celtis* (2.95%)	Cyperaceae (5.67%)	*Sebastiania* (4.60%)	*Celtis* (6.03%)

Table 7.1. The dominant pollen taxa from artificial pollen traps from savanna and SDTF ecosystems within NKMNP.

modern pollen rain. The study shows that the modern pollen rain of the ecosystems differs both spatially and temporally and emphasises the importance of using numerous artificial pollen traps from one site and sampling over a period of several years.

A comparison between the modern pollen rain from surface lake sediments and artificial pollen traps shows that although differences exist in the pollen profiles of these samples, both sampling methods show similar taxa for each ecosystem. This implies that artificial pollen traps can be a useful method to aid the interpretation of fossil pollen records.

The modern pollen spectra described in this thesis were applied to fossil pollen records in chapter six to strengthen the interpretation of these records. For example, modern pollen spectra were compared with fossil pollen spectra from Laguna La Gaiba (B. Whtiney, unpublished data) in the Bolivian Pantanal to show the development of upland SDFT around the lake during the Holocene and the presence of open ecosystems for most of the Pleistocene record. Within NKMNP in eastern Bolivia (Mayle *et al.,* 2000; Burbridge *et al.,* 2004), the occurance of *Curatella americana* in the modern pollen rain of both upland savannas and seasonally-flooded savannas, means that the Early Holocene record may not necessarily solely reflect seasonally-flooded savannas but possibly also areas of upland savannas on elevated regions around the lake. The plausability of the "Pleistocene Dry Forest Arc" theory (Prado and Gibbs, 1993; Mayle, 2006) in the southern Neotropics may be investigated using *Anadenanthera* as a pollen taxon representative of upland SDTF ecosystems, allowing the recognition of these ecosystems in fossil pollen records.

7.3. Critical analysis of the methodology

Artificial pollen traps allowed the modern pollen rain of the ecosystems to be captured effectively, as the majority of the prepared pollen traps contained enough well-preserved

pollen to allow the pollen sum of 300 grains to be reached. The percentage of unidentifiable, poorly preserved grains was generally less than 20%, indicating that pollen was fairly well preserved within the artificial pollen traps. One possible problem with the use of these pollen traps was that they were located 0.5 m above ground level or the seasonal-inundation level. This means that any poorly dispersed pollen from small herbs may not be effectively captured by the pollen traps as the flowers would be well below the sampling height. This effect could have been of particular importance in the savanna ecosystems due to the well developed ground flora. For the sampling of ecosystems with a significant ground cover, e.g. seasonal forests and savannas, it may be preferable to position the traps upon the ground to allow more of this poorly dispersed pollen to be captured, providing that the trap could be kept clear of leaf litter. Pollen trapping programs in other studies have placed the pollen traps at ground level (Hicks *et al.,* 2008). However, the placing of traps on the ground would only be possible for *terra firme* sites, as pollen traps in seasonally-inundated sites would be flooded by water containing a regional pollen signal. Hence, for inundated sites the placement of traps above the inundation level appears to be the most effective method of capturing the ecosystem pollen signal.

Fire damage was a major factor which affected the recovery of the pollen traps from the upland savanna (*campo cerrado*) site. Although the traps were raised above the ground level, all traps from the 2000 sampling season were destroyed by the fire. It seems that merely raising the traps above ground level is not sufficient to prevent fire damage in savanna ecosystems.

A major issue with regard to the applicability of the modern pollen rain spectra from the artificial pollen traps is that they are collected from a different sampling environment from fossil pollen records, which are commonly collected from lake sediments. The lake samples will contain pollen of both air-borne and water-borne components as well as pollen directly deposited into the lake by aquatic plants and shoreline vegetation, whereas the pollen traps will only capture an air-borne pollen component. Although,

ideally, numerous modern pollen spectra would be obtained from surface lake sediments, the paucity of lakes in some vegetation formations (e.g. upland savanna) and accessibility issues when working in remote areas of the Neotropics limits the feasibility of this approach. Artificial pollen traps also have the advantage of providing modern pollen/vegetation relationships and an understanding of pollen influx rates as the duration of pollen deposition is known for pollen traps. Both these attributes are very difficult to calculate accurately when using surface lake sediments. However, as similarities were recorded in the modern pollen spectra of an ecosystem, whether the data were obtained from surface lake sediments or pollen traps (section 5.6.8), it appears that pollen trap data is suitable for comparing with data from fossil pollen records from lake sediments. However, when using the modern pollen spectra from artificial pollen traps such as those presented in this thesis as an interpretation aid for fossil pollen records from lake sediments, it is important to consider the aforementioned factors regarding pollen source area.

The vegetation inventories of the forest plots used in this research only included those plants with a diameter at breast height ≥ 10 cm. This was problematic as the modern pollen rain of the ecosystem includes pollen produced from any plant within the ecosystem, not just those with a dbh ≥10 cm. Therefore, the modern pollen/vegetation ratios could not be calculated for those individuals which may have been present within the vegetation plots but only as herbs, shrubs or small trees with a dbh <10 cm. An example from the upland SDTF plot would be Bromeliaceae which occur as herbs with a dbh <10 cm, hence were not included within the vegetation survey. For future modern pollen rain studies from forest ecosystems with a significant ground cover (e.g. SDTF), it would be advisable to sample a wider range of individuals within the vegetation plot. This could be achieved by using a smaller dbh numeric (e.g. sampling all individuals with a dbh ≥ 2.5 cm, rather than a dbh ≥ 10 cm as in this study), or through the use of nested quadrats, where different sized quadrats are used to sample the ground flora and the woody flora of a vegetation plot (Kent and Coker, 1992).

7.4. Possible future research

The difficulty of separating different types of savanna by their modern pollen rain observed in this research means palaeoecological proxies other than pollen may be more suitable for achieving this aim. Phytoliths (particles of biogenic silica produced in the leaves of grasses) and grass cuticles both have a greater degree of morphological variability relative to grass pollen and have shown the potential to improve the reconstruction of grass dominated ecosystems (Wooler, 2002). Both these methods have been used effectively to reconstruct the vegetation history of some grassland areas in much more detail than the authors believe would be achievable through pollen analysis (Blinnikov *et al.,* 2002; Scott, 2002).

The modern pollen rain signal of the seasonally-inundated SDTF ecosystem is currently of rather unknown geographic applicability due to the limited ecological knowledge of this type of ecosystem with Bolivia (Killeen, 1998; Navarro and Maldonado, 2005). More detailed ecological and botanical studies would allow the floristic variability and ecological preferences (e.g. edaphic conditions, climatic regime) of this ecosystem to be known in much more detail. This would aid the palaeoclimatic interpretations from fossil pollen records if the pollen signal suggested the existence of a type of seasonally-inundated SDTF.

Another issue from this research was the high proportions of grains which could not be reliably identified to any specific taxonomic group, or could only be identified to family level, which limits the ecological interpretation of the pollen spectra. This issue could be minimised through increasing the size and dissemination of modern pollen reference collections for neotropical plant species via electronic databases (e.g. Bush and Weng, 2007). There is also a requirement for more detailed morphological studies on pollen grains from plant families which are commonly found within palynological records but at present may only be identified with low taxonomic resolution. Recent research has shown the potential of separating the Moraceae/Urticaceae pollen group to generic level

resolution (Burn and Mayle. 2008). Another group of particular interest are the Combretaceae and Melastomataceae families, which at present are very difficult to differentiate on the basis of their pollen grain morphology. Hence the pollen group Combretaceae/Melastomataceae is of little ecological significance at such a coarse taxonomic resolution due to species of these two families being found in a wide range of habitats (Marchant *et al.,* 2002).

References

Adams, J. M., and Faure, H. (1998). A new estimate of changing carbon storage on land since the last glacial maximum, based on global land ecosystem reconstruction. *Global and Planetary Change* **16-17,** 3-24.

Alverson. (2004). Bombacaceae. *In* "Flowering Plants of the Neotropics." (N. Smith, S. Mori, A, A. Henderson, D. W. Stevenson, and S. V. Heald, Eds.), pp. 55-58. Princeton University Press, Oxford.

Assine, M. L., and Soares, P. C. (2004). Quaternary of the Pantanal, west-central Brazil. *Quaternary International* **114,** 23-34.

Autio, J., and Hicks, S. (2004). Annual variations in pollen deposition and meteorological conditions on the fell Aakenustunturi in northern Finland: Potential for using fossil pollen as a climate proxy. *Grana* **43,** 31-47.

Barberi, M., Salgado-Labouriau, M. L., and Suguio, K. (2000). Paleovegetation and paleoclimate of "Vereda de Águas Emendadas", central Brazil. *Journal of South American Earth Sciences* **13,** 241-254.

Bawa, K. S., Bullock, S. H., Perry, D. R., Coville, R. E., and Grayum, M. H. (1985). Reproductive biology of tropical lowland rain forest trees. II. Pollination systems. *American Journal of Botany* **72,** 346-356.

Beck, S. G., and Moraes R, M. (2004). Características biológicas generales de la llanura del Beni. *In* "Diversidad Biológica en las Llanura de Inundación del Río Mamoré" (M. Pouilly, S. G. Beck, M. Moraes R, and C. Ibanez, Eds.), pp. 27-76. Centro de Ecología Simón I. Patiño, Santa Cruz, Bolivia.

Behling, H. (1995). A high resolution Holocene pollen record from Lago do Pires, SE Brazil: vegetation, climate and fire history. *Journal of Paleolimnology* **14,** 253-268.

Behling, H. (2002). South and southeast Brazilian grasslands during Late Quaternary times: a synthesis. *Palaeogeography, Palaeoclimatology, Palaeoecology* **177,** 19-27.

Behling, H., and Hooghiemstra, H. (1999). Environmental history of the Colombian savannas of the Llanos Orientales since the Last Glacial Maximum from lake records El Pinal and Carimagua. *Journal of Paleolimnology* **21,** 461-476.

Behling, H., and Hooghiemstra, H. (2000). Holocene Amazon rainforest-savanna dynamics and climatic implications: high-resolution pollen record from Laguna Loma Linda in eastern Colombia. *Journal of Quaternary Science* **15,** 687-695.

Berg, C. (2004a). Moraceae. *In* "Flowering Plants of the Neotropics." (N. Smith, S. Mori, A, A. Henderson, D. W. Stevenson, and S. V. Heald, Eds.), pp. 253-256. Princeton University Press, Oxford.

Berg, C. (2004b). Urticaceae. *In* "Flowering Plants of the Neotropics." (N. Smith, S. Mori, A, A. Henderson, D. W. Stevenson, and S. V. Heald, Eds.), pp. 384-385. Princeton University Press, Oxford.

Berg, C. (2004c). Cecropiaceae. *In* "Flowering Plants of the Neotropics." (N. Smith, S. Mori, A, A. Henderson, D. W. Stevenson, and S. V. Heald, Eds.), pp. 92-94. Princeton University Press, Oxford.

Berrio, J. C., Hooghiemstra, H., Behling, H., Botero, P., and Van der Borg, K. (2002). Late-Quaternary savanna history of the Colombian Llanos Orientales from Lagunas Chenevo and Mozambique: a transect synthesis. *The Holocene* **12,** 35-48.

Birks, H., J, B, and Gordon, A. D. (1985). "Numerical Methods in Quaternary Pollen Analysis." Academic Press, London.

Birks, H. J. B., and Birks, H. H. (1980). "Quaternary Palaeoecology." Edward Arnold, London.

Birks, H. J. B. (1986). Numerical zonation, comparison and correlation of Quaternary stratigraphical data. *In* "Handbook of Holocene Palaeoecology and Palaeohydrology." (B. Berglund, E, Ed.), pp. 743-774. John Wiley & Sons, Chichester.

Blinnikov, M., Busacca, A., and Whitlock, C. (2002). Reconstruction of the late Pleistocene grassland of the Columbia basin, Washington, USA, based on phytolith records in loess. *Palaeogeography, Palaeoclimatology, Palaeoecology* **177,** 77-101.

Burbridge, R. E., Mayle, F. E., and Killeen, T. J. (2004). Fifty-thousand-year vegetation and climate history of Noel Kempff Mercado National Park, Bolivian Amazon. *Quaternary Research* **61,** 215-230.

Burn, M. J. (2008). "Palynological Characterisation of Amazonian Rainforest Communities, NE Bolivia". Unpublished PhD thesis, University of Edinburgh.

Burn, M. J., and Mayle, F. E. (2008). Palynological differentiation between genera of the Moraceae family and implications for Amazonian palaeoecology. *Review of Palaeobotany and Palynology* **149,** 187-201.

Bush, M., and Rivera, R. (1998). Pollen dispersal and representation in a neotropical rain forest. *Global Ecology and Biogeography* **7,** 379-392.

Bush, M. B. (1991). Modern pollen-rain data from South and Central America: a test of the feasibility of fine-resolution lowland tropical palynology. *The Holocene* **1,** 162-167.

Bush, M. B. (1992). A simple yet efficient pollen trap for use in vegetation studies. *Journal of Vegetation Science* **3,** 275-276.

Bush, M. B. (1994). Amazonian speciation: A necessarily complex model. *Journal of Biogeography* **21,** 5-17.

Bush, M. B. (1995). Neotropical plant reproductive strategies and fossil pollen representation. *The American Naturalist* **145,** 594-609.

Bush, M. B. (2002). On the interpretation of fossil Poaceae pollen in the lowland humid Neotropics. *Palaeogeography, Palaeoclimatology, Palaeoecology* **177,** 5-17.

Bush, M. B., De Oliveira, P. E., Colinvaux, P. A., Miller, M. C., and Moreno, J. E. (2004). Amazonian paleoecological histories: one hill, three watersheds. *Palaeogeography, Palaeoclimatology, Palaeoecology* **214,** 359-393.

Bush, M. B., Miller, M. C., De Oliveira, P. E., and Colinvaux, P. A. (2000). Two histories of environmental change and human disturbance in eastern lowland Amazonia. *The Holocene* **10,** 543-553.

Bush, M. B., and Silman, M. R. (2004). Observations on Late Pleistocene cooling and precipitation in the lowland Neotropics. *Journal of Quaternary Science* **19,** 677-684.

Bush, M. B., and Weng, C. (2007). Introducing a new (freeware) tool for palynology. *Journal of Biogeography* **34,** 377-380.

Caetano, S., Prado, D., Pennington, R. T., Beck, S., Oliveira-Filho, A., Spichiger, R., and Naciri, Y. (2008). The history of Seasonally Dry Tropical Forests in eastern South America: inferences from the genetic structure of the tree *Astronium urundeuva* (Anacardiaceae). *Molecular Ecology* **17,** 3147-3159.

Cavalcanti, R. B., and Joly, C. A. (2002). Biodiversity and conservation priorities in the cerrado region. *In* "The Cerrados of Brazil." (P. S. Oliveira, and R. J. Marquis, Eds.), pp.

351-368. Columbia University Press, New York.

Clapperton, C. M. (1993). Nature of environmental changes in South America at the Last Glacial Maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology* **101,** 189-208.

Colinvaux, P. A., De Oliveira, P. E., and Bush, M. B. (2000). Amazonian and neotropical plant communities on glacial time-scales: The failure of the aridity and refuge hypotheses. *Quaternary Science Reviews* **19,** 141-169.

Colinvaux, P. A., De Oliveira, P. E., Moreno, J. E., Miller, M. C., and Bush, M. B. (1996). A long pollen record from Lowland Amazonia: Forest and cooling in glacial times. *Science* **274,** 85-88.

Colinvaux, P. A., De Oliveira, P. E., and Patino, J. E. M. (1999). "Amazon Pollen Manual and Atlas." Harwood Academic Publishers, Amsterdam.

Daly, D.C. (2004). Lacistemataceae. *In* "Flowering Plants of the Neotropics." (N. Smith, S. Mori, A, A. Henderson, D. W. Stevenson, and S. V. Heald, Eds.), pp. 200-201. Princeton University Press, Oxford.

Davis, J. I. (2004). Poaceae. *In* "Flowering Plants of the Neotropics." (N. Smith, S. Mori, A, A. Henderson, D. W. Stevenson, and S. V. Heald, Eds.), pp. 470-473. Princeton University Press, Oxford.

Davis, M. B. (1963). On the theory of pollen analysis. *American Journal of Science* **261,** 897-912.

Davis, M. B., Brubaker, L. B., and Beiswenger, J. M. (1971). Pollen grains in lake sediments: Pollen percentages in surface sediments from southern Michigan. *Quaternary*

Research **1,** 450-467.

Denevan, W. M. (1970). Aboriginal drained-field cultivation in the Americas. *Science* **169,** 647-654.

Dimbleby, G.W. (1957). Pollen analysis of terrestrial soils. *New Phytologist* **56,** 12-28.

Diniz de Araujo Neto, M., Furley, P. A., Haridasan, M., and Johnson, C. E. (1986). The murundus of the cerrado region of Central Brazil. *Journal of Tropical Ecology* **2,** 17-35.

Durigan, A., and Ratter, J. A. (2006). Successional changes in cerrado and cerrado/forest ecotonal vegetation in western Sao Paulo State, Brazil, 1962-2000. *Edinburgh Journal of Botany* **63,** 119-130.

Eiten, G. (1972). Cerrado vegetation of Brazil. *Botanical Review* **38,** 303-320.

Eva, H.D., Belward, A. S., De Miranda, E. E., Di Bella, C. M., Gond, V., Huber, O., Jones, S., Sgrenzaroli, M., and Fritz, S. (2004). A land cover map of South America. *Global Change Biology* **10,** 731-744.

Faegri, K., and Iversen, K. (1989). "Textbook of Pollen Analysis." Blackburn Press, New Jersey.

Ferraz-Vicentini, K. R., and Salgado-Labouriau, M. L. (1996). Palynological analysis of a palm swamp in Central Brazil. *Journal of South American Earth Sciences* **9,** 207-219.

Ferreira-Júnior., W. G., Silva, A. F., Schaefer, C. E. G. R., Meira Neto, J. A. A., Dias, A. S., Ignácio, M., and Medeiros, M. C. M. P. (2007). Influence of soils and topographic gradients on tree species distribution in a Brazilian Atlantic semideciduous forest. *Edinburgh Journal of Botany* **64,** 137-157.

Filgueiras, T. S. (2002). Herbaceous plant communities. *In* "The Cerrados of Brazil." (P. S. Oliveira, and R. J. Marquis, Eds.), pp. 121-139. Columbia University Press, New York.

Fontana, S. L. (2003). Pollen deposition in coastal dunes, south Buenos Aires Province, Argentina. *Review of Palaeobotany and Palynology* **126,** 17-37.

Fowler, J., Cohen, L., Jarvis, P. (1998). "Practical Statistics for Field Biology". 2nd Edition. John Wiley & Sons, Chichester.

Furley, P. A. (1986). Classification and distribution of murundus in the cerrado of Central Brazil. *Journal of Biogeography* **13,** 265-268.

Furley, P. A. (1999). The nature and diversity of neotropical savanna vegetation with particular reference to the Brazilian cerrados. *Global Ecology and Biogeography* **8,** 223-241.

Furley, P. A., and Ratter, J. A. (1988). Soil resources and plant communities of the Central Brazilian cerrado and their development. *Journal of Biogeography* **15,** 97-108.

Furley, P. A., and Ratter, J. A. (1990). Pedological and botanical variations across the forest-savanna transition on Maraca Island. *The Geographical Journal* **156,** 251-266.

Gentry, A.H. (1993). "A Field Guide to the Families and Genera of Woody Plants of Northwest South America (Colombia, Ecuador, Peru), with Supplementary Notes on Herbaceous Vegetation". University of Chicago Press, Chicago.

Gosling, W. D. (2004). "Characterisation of Neotropical Forest and Savannah Ecosystems by their Modern Pollen Rain." Unpublished PhD thesis, University of Leicester.

Gosling, W. D., Mayle, F. E., Killeen, T. J., Siles, M., Sanchez, L., and Boreham, S. (2003). A simple and effective methodology for sampling modern pollen rain in tropical environments. *Holocene* **13,** 613-618.

Gosling, W. D., Mayle, F. E., Tate, N. J., and Killeen, T. J. (2005). Modern pollen-rain characteristics of tall terra firme moist evergreen forest, southern Amazonia. *Quaternary Research* **64,** 284-297.

Gosling, W. D., Mayle, F. E., Tate, N. J., and Killeen, T. J. (2008). Differentiation between neotropical rainforest, dry forest, and savannah ecosystems by their modern pollen spectra and implications for the fossil pollen record. *Review of Palaeobotany and Palynology* doi:10.1016/j.revpalbo.2008.06.007

Graham, S. A., Nowicke, J., Skvarla, J. J., Graham, S. A., Patel, V., and Lee, S. (1985). Palynology and systematics of the Lythraceae. I. Introduction and genera *Adenaria* through *Ginoria*. *American Journal of Botany* **72,** 1012-1031.

Graham, S. A. (2004). Lythraceae. *In* "Flowering Plant Families of the Neotropics." (N. Smith, S. Mori, A, A. Henderson, D. W. Stevenson, and S. V. Heald, Eds.), pp. 223-225. Princeton University Press, Oxford.

Gribel, R., and Hay, J. D. (1993). Pollination ecology of *Caryocar brasiliense* (Caryocaraceae) in Central Brazil cerrado vegetation. *Journal of Tropical Ecology* **9,** 199-211.

Haberle, S. G., and Maslin, M. A. (1999). Late Quaternary vegetation and climate change in the Amazon Basin based on a 50,000 year pollen record from the Amazon Fan, ODP Site 932. *Quaternary Research* **51,** 27-38.

Haffer, J. (1969). Speciation in Amazonian forest birds. *Science* **165,** 131-137.

Hanagarth, W. (1993). "Acerca de la Geoecología de las Sabanas del Beni en Noreste de Bolivia." Instituto de Ecología, Universidad Mayor de San Andrés, La Paz, Bolivia.

Henriques, R. P. B., and Hay, J. D. (2002). Patterns and dynamics of plant population. *In* "The Cerrados of Brazil." (P. S. Olveira, and R. J. Marquis, Eds.), pp. 140-158. Columbia University Press, New York.

Hicks, S. (1999). The relationship between climate and annual pollen deposition at northern tree-lines. *Chemosphere - Global Change Science* **1,** 403-416.

Hicks, S. (2001). The use of annual arboreal pollen deposition values for delimiting tree-lines in the landscape and exploring models of pollen dispersal. *Review of Palaeobotany and Palynology* **117,** 1-29.

Hicks, S., Ammann, B., Latalowa, M., Pardoe, H., and Tinsley, H. (2008). European Pollen Monitoring Program. http://wdc.obs-mip.fr/pmp/guide.html.

Hoffmann, W. A., and Moreira, A. G. (2002). The role of fire in population dynamics of woody plants. *In* "The Cerrados of Brazil." (P. S. Oliveira, and R. J. Marquis, Eds.), pp. 159-177. Columbia University Press, New York.

Huber, O., Duno de Stefano, R., Aymard, G., and Riina, R. (2006). Flora and vegetation of the Venezuelan Llanos. *In* "Neotropical Savannas and Seasonally Dry Tropical Forests: Diversity, Biogeography and Conservation." (R. T. Pennington, G. P. Lewis, and J. A. Ratter, Eds.), pp. 95-120. CRC Press, Boca Raton, USA.

ILDIS. (2008). International Legume and Database Service. http://www.ildis.org. Accessed 29-08-08.

IPCC. (2007). "Climate Change 2007: Contribution of Working Group 1 to the Fourth

Assessment Report of the Intergovernmental Panel on Climate Change." Cambridge University Press, Cambridge, UK.

Jardim, A., Killeen, T. J., and Fuentes, A. (2003). "Guia de los Arboles y Arbustos del Bosque Seco Chiquitano, Bolivia." Editorial FAN, Santa Cruz, Bolivia.

Juggins, S. (2003). "C2. Software for ecological and palaeoecological data analysis and visualisation". University of Newcastle, Newcastle upon Tyne, UK.

Kawasaki, M. L., and Holst, B. K. (2004). Myrtaceae. *In* "The Flowering Plants of the Neotropics." (N. Smith, S. Mori, A, A. Henderson, D. W. Stevenson, and S. V. Heald, Eds.), pp. 264-266. Princeton University Press, Oxford.

Kent, M., and Coker, P. (1992). "Vegetation Description and Analysis: A Practical Approach." John Wiley and Sons, Chichester.

Killeen, T. J. (1998). Vegetation and flora of Parque Nacional Noel Kempff Mercado. *In* "A Biological Assessment of Parque Nacional Noel Kempff Mercado, Bolivia. RAP working papers 10." (T. J. Killeen, and T. S. Schulenberg, Eds.), pp. 61-88. Conservation International, Washington, D.C.

Killeen, T. J., Chavez, E., Pena-Claros, M., Toledo, M., Arroyo, L., Caballero, J., Correa, L., Guillen, R., Quevedo, R., Saldias, M., Soria, L., Uslar, Y., Vargas, I., and Steininger, M. (2006). The Chiquitano dry forest, the transistion between humid and dry forest in Eastern Lowland Bolivia. *In* "Neotropical Savannas and Seasonally Dry Tropical Forests: Plant Diversity, Biogeography and Conservation." (R. T. Pennington, G. P. Lewis, and J. A. Ratter, Eds.), pp. 213-234. CPC Press, Boca Raton, USA.

Killeen, T. J., Jardim, A., Mamani, F., and Rojas, N. (1998). Diversity, composition and structure of a tropical semideciduous forest in the Chiquitanía region of Santa Cruz,

Bolivia. *Journal of Tropical Ecology* **14,** 803-827.

Killeen, T. J., and Schulenberg, T. S. (1998). A Biological Assessment of Parque Nacional Noel Kempff Mercado, Bolivia. RAP working papers 10. Conservation International, Washington D.C.

Killeen, T. J., Siles, T. M., Grimwood, T., Tieszen, L. L., Steininger, M. K., Tucker, C. J., and Panfil, S. J. (2003). Habitat heterogeneity on a forest-savanna in Noel Kempff Mercado National Park (Santa Cruz, Bolivia): Implications for the long-term conservation of biodiversity in a changing climate *In* "How Landscapes Change." (G. A. Bradshaw, and P. A. Marquety, Eds.), pp. 285-312. Springer-Verlag, Berlin.

Langstroth, R. P. (1996). "Forest islands in an Amazonian savannah of northeastern Bolivia." Unpublished PhD thesis, University of Washington-Madison.

Ledru, M.-P. (2002). Late Quaternary history and evolution of the cerrados as revealed by palynological records. *In* "The Cerrados of Brazil." (P. S. Oliveria, and R. J. Marquis, Eds.), pp. 33-51. Columbia University Press, New York.

Ledru, M.-P., Ceccantini, G., Gouveia, S. E. M., López-Sáez, J. A., Pessenda, L. C. R., and Ribeiro, A. S. (2006). Millenial-scale climatic and vegetation changes in a northern Cerrado (Northeast, Brazil) since the Last Glacial Maximum. *Quaternary Science Reviews* **25,** 1110-1126.

Linder, H. P., and Rudall, P. J. (2005). Evolutionary history of Poales. *Annual Review of Ecology, Evolution, and Systematics* **36,** 107-124.

Lowe, J. J., and Walker, J. W. C. (1997). "Reconstructing Quaternary Environments." Pearson Education Limited, Harlow.

Madriñan, S. (2004). Lauraceae. *In* "Flowering Plants of the Neotropics." (N. Smith, S. Mori, A, A. Henderson, D. W. Stevenson, and S. V. Heald, Eds.), pp. 204-206. Princeton University Press, Oxford.

Male, T. (2001). Terrestrial Ecoregions – Pantanal. http://www.nationalgeographic.com/wildworld/terrestrial.html. Accessed 29-08-08

Malhi, Y., Roberts, J. T., Betts, R. A., Killeen, T. J., Li, W., and Nobre, C. A. (2008). Climate Change, Deforestation, and the Fate of the Amazon. *Science* **319,** 169-172.

Marchant, R., Almeida, L., Behling, H., Berrio, J. C., Bush, M., Cleef, A., Duivenvoorden, J., Kappelle, M., De Oliveira, P., Teixeira de Oliveira-Filho, A., Lozano-Garcia, S., Hooghiemstra, H., Ledru, M.-P., Ludlow-Wiechers, B., Markgraf, V., Mancini, V., Paez, M., Prieto, A., Rangel, O., and Salgado-Labouriau, M. L. (2002). Distribution and ecology of parent taxa of pollen lodged within the Latin American Pollen Database. *Review of Palaeobotany and Palynology* **121,** 1-75.

Mann, C. C. (2008). Archaeology: Ancient earthmovers of the Amazon. *Science* **321,** 1148-1152.

Marimon, B. S., Felfili, J. M., and Lima, E. S. (2002). Floristics and phytosociology of the gallery forest of the Babaca Stream, Nova Xavantina, Mato Grosso, Brazil. *Edinburgh Journal of Botany* **59,** 303-318.

Martins, F. Q., and Batalha, M. A. (2006). Pollination systems and floral traits in cerrado woody species of the Upper Taquari region (central Brazil). *Brazilian Journal of Biology* **66,** 543-552.

Mayle, F. E. (2004). Assessment of the Neotropical dry forest refugia hypothesis in the light of palaeoecological data and vegetation model simulations. *Journal of Quaternary*

Science **19,** 713-720.

Mayle, F. E. (2006). The Late Quaternary biogeographic history of South American seasonally dry tropical forests: Insights from palaeo-ecological data. *In* "Neotropical Savannas and Seasonally Dry Forests: Plant diversity, Biogeography and Conservation." (R. T. Pennington, G. P. Lewis, and J. A. Ratter, Eds.). CRC Press, Boca Raton, USA.

Mayle, F. E., and Beerling, D. J. (2004). Late Quaternary changes in Amazonian ecosystems and their implications for global carbon cycling. *Palaeogeography, Palaeoclimatology, Palaeoecology* **214,** 11-25.

Mayle, F. E., Beerling, D. J., Gosling, W. D., and Bush, M. B. (2004). Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. *Philosophical Transactions of the Royal Society B: Biological Sciences* **359,** 499-514.

Mayle, F. E., Burbridge, R., and Killeen, T. J. (2000). Millennial-Scale dynamics of Southern Amazonian rain forests. *Science* **290,** 2291-2294.

Mayle, F. E., and Power, M. J. (2008). Impact of a drier Early–Mid-Holocene climate upon Amazonian forests. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363,** 1829-1838.

Mooney, H. A., Bullock, S. H., and Medina, E. (1995). Introduction. *In* "Seasonally Dry Tropical Forests." (H. A. Mooney, S. H. Bullock, and E. Medina, Eds.), pp. 1-8. Cambridge, Cambridge University Press.

Moore, P. D., Webb, J. A., and Collinson, M. D. (1991). "Pollen Analysis." Blackwell, Oxford.

Munhoz, C. B. R., and Felfili, J. M. (2006). Floristics of the herbaceous and subshrub layer of moist grassland in the cerrado biosphere reserve (Alto Paraiso de Goias), Brazil. *Edinburgh Journal of Botany* **62,** 343-354.

Navarro, G., and Maldonado, M. (2005). "Geografia, Ecológica de Bolivia: Vegetación y Ambientes Acuáticos." Centro de Ecología Simón I. Patiño, Santa Cruz, Bolivia.

Oksanen, J., Kindt, R., Legendre, P., and O'Hara, R. B. (2007). "Vegan: Community Ecology Package version 1.8-5." http://cran.r-project.org

Oliveira-Filho, A., and Ratter, J. A. (1995). A study of the origin of Central Brazilian forests by the analysis of plant species distribution patterns. *Edinburgh Journal of Botany* **52,** 141-194.

Oliveira-Filho, A. T. d., and Ratter, J. A. (2002). Vegetation physiognomies and woody flora of the Cerrado Biome. *In* "The Cerrados of Brazil." (P. S. Oliveira, and R. J. Marquis, Eds.). Columbia University Press, New York.

Oliveira-Filho, A. T. d. (1992a). Floodplain 'Murundus' of Central Brazil: Evidence for the Termite-Origin Hypothesis. *Journal of Tropical Ecology* **8,** 1-19.

Oliveira-Filho, A. T. d. (1992b). The Vegetation of Brazilian 'Murundus'-the island-effect on the plant community. *Journal of Tropical Ecology* **8,** 465-486.

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., John F. Lamoreux, J. F., Wettengel, W. W., Hedao, P., and Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on Earth a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *Bioscience* **51,** 933-939.

Orellana, M. R., Beck, S. G., and Bourrel, L. (2004). Unidades majores de vegetación de las sabanas. *In* " Diversidad Biológica en la Llanura de Inundación del Río Mamoré". (M. Pouilly, S. G. Beck, M. Moares R, and I. C, Eds.), pp. 141-166. Centro de Ecología Simón I. Patiño, Santa Cruz, Bolivia.

Panfil, S. (2001). "Late Holocene Forest and Savanna Diversity and Dynamics Across an Amazonian Ecotone." Unpublished PhD thesis, University of Georgia.

Parker T.A., I., Gentry, A. H., Foster, R. B., Emmons, L. H., and Remsen, J., J.V (1993). "The Lowland Dry Forests of Santa Cruz, Bolivia: A Global Conservation Priority." Conservation International, Washington D.C.

Pennington, R. T., Lewis, G.P., and Ratter, J. A. (2006). An overview of plant diversity, biogeography and conservation of neotropical savannas and seasonally dry forests. *In* "Neotropical Savannas and Seasonally Dry Forests: Plant diversity, Biogeography and Conservation." (R. T. Pennington, G.P. Lewis and J. A. Ratter, Eds.), pp. 1-30. CRC Press, Boca Raton, USA.

Pennington, R. T., Lavin, M., Prado, D. E., Pendry, C. A., Pell, S. K., and Butterworth, C. A. (2004). Historical climate change and speciation: neotropical seasonally dry forest plants show patterns of both Tertiary and Quaternary diversification. *Philosophical Transactions of the Royal Society B: Biological Sciences* **359,** 515-538.

Pennington, R. T., Prado, D. E., and Pendry, C. A. (2000). Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography* **27,** 261-273.

Pinder, L., and Rosso, S. (1998). Classification and ordination of plant formations in the Pantanal of Brazil. *Plant Ecology* **136,** 151-165.

Pinto, R. R., Oliverirs-Filho, A. T., and Hay.D.V. (2005). Influence of soil and

topography on the composition of a tree community in a Central Brazilian valley forest. *Edinburgh Journal of Botany* **62,** 69-90.

Ponce, M., Da Cunha, C.A. (1993) Vegetated earthmounds in tropical savannas of central Brazil: A synthesis with special reference to the Pantanal do Mato Grosso *Journal of Biogeography* **20:22**, 219-225,

Prado, D. E. (2000). Seasonally dry forests of tropical South America: from forgotten ecosystems to a new phytogeographic unit. *Edinburgh Journal of Botany* **57,** 437-461.

Prado, D. E., and Gibbs, P. E. (1993). Patterns of species distributions in the dry seasonal forests of South America. *Annals of the Missouri Botanical Garden* **80,** 902-927.

Prance, G., and Schaller, G. (1982). Preliminary study of some vegetation types of the Pantanal, Mato Grosso, Brazil. *Brittonia* **34,** 228-251.

Prentice, I. C. (1986). Multivariate methods for data analysis. *In* "Handbook of Holocene Palaeoecology and Palaeohydrology." (B. Berglund , E, Ed.), pp. 775-797. John Wiley and Sons, Chichester.

Pruski, J. F., and Sancho, G. (2004). Asteraceae. *In* "Flowering Plants of the Neotropics." (N. Smith, S. Mori, A, A. Henderson, D. W. Stevenson, and S. V. Heald, Eds.), pp. 33-39. Princeton University Press, Princeton.

R Development Core Team. (2007). R: A language and environment for statistical computing. R Foundation for statistical computing.

Ramírez, N. (2004). Ecology of pollination in a tropical Venezuelan savanna. *Plant Ecology* **173,** 171-189.

Ratter, J. A. (1992). Transitions between cerrado and forest vegetation in Brazil. *In* "Nature and Dynamics of Forest-Savanna boundaries." (P. A. Furley, J. Proctor, and J. A. Ratter, Eds.) pp.417-430. Chapman and Hall, London.

Ratter, J. A., Askew, G. P., Montgomery, R. F., and Gifford, D. R. (1978). Observations on the Vegetation of Northeastern Mato Grosso. II. Forests and Soils of the Rio Suia-Missu Area. *Proceedings of the Royal Society of London. Series B, Biological Sciences* **203,** 191-208.

Ratter, J. A., Bridgewater, S., Atkinson, R., and Ribeiro, J. F. (1996). Analysis of the floristic composition of the Brazilian cerrado vegetation II: comparison of the woody vegetation of 98 areas. *Edinburgh Journal of Botany* **53,** 153-180.

Ratter, J. A., Bridgewater, S., and Ribiero, J. F. (2003). Analysis of the floristic composition of the Brazilian cerrado vegetation III: Comparison of the woody flora of 376 areas. *Edinburgh Journal of Botany* **60,** 57-109.

Ratter, J. A., Pott, A., Pott, V. J., Cunha, C. N. d., and Hardisan, M. (1988). Observations on woody vegetation types in the Pantanal and Corumba, Brazil. *Notes from the Royal Botanic Garden, Edinburgh,* **45,** 503-525.

Ratter, J. A., Ribeiro, J. F., and Bridgewater, S. (1997). The Brazilian cerrado vegetation and threats to its biodiversity. *Annals of Botany* **80,** 223-230.

Ratter, J. A., Richards, P. W., Argent, G., and Gifford, D. R. (1973). Observations on the vegetation of Northeastern Mato Grosso: I. The woody vegetation types of the Xavantina-Cachimbo Expedition Area. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **266,** 449-492.

Reese, C. A., and Liu, K.-b. (2005). A modern pollen rain study from the central Andes

region of South America. *Journal of Biogeography* **32,** 709-718.

Renner, S. S. (2004). Melastomataceae. *In* "Flowering Plant Families of the Neotropics." (N. Smith, S. Mori, A, A. Henderson, D. W. Stevenson, and S. V. Heald, Eds.), pp. 240-243. Princeton University Press, Oxford.

Ritchie, J. C., and Yarranton, G. A. (1978). The Late-Quaternary history of the Boreal Forest of Central Canada, based on standard pollen stratigraphy and principal components analysis. *The Journal of Ecology* **66,** 199-212.

Rodgers, J. C., and Horn, S. P. (1996). Modern pollen spectra from Costa Rica. *Palaeogeography, Palaeoclimatology, Palaeoecology* **124,** 53-71.

Roubik, D. W., and Moreno, J. E. (1991). "Pollen and Spores of Barro Colorado Island." Missouri Botanical Garden, St Louis.

Salgado-Labouriau, M.L. (1973). Contibuicao a Palinologia dos Cerrados. Academia Brasileria de Ciancias, Rio de Janerio, Brazil.

Salgado-Labouriau, M. L. (1978). Pollen and spore rain in Central Brazil. *In* "The 1st. International Conference on Aerobiology." (Lauer, Ed.), pp. 89–101. Federal Environmental Agency, Berlin.

SALVIAS. (2002 and onwards). The SALVIAS project. Accessed 01-09-05. http://www.salvias.net, http://www.salvias.net.

Sanjinés, A., and Beck, S. G. (2004). Vegetación acuática y ribereña de las lagunas. *In* "Diversidad Biológica en la Llanura de Inundación del Río Mamoré." (M. Pouilly, S. G. Beck, R. M. Morares, and C. Ibanez, Eds.), pp. 193-234. Centro de Ecología Simón I. Patiño, Santa Cruz, Bolivia.

Sarmiento, G. (1984). "The Ecology of Neotropical Savannas." Harvard University Press, Cambridge, USA.

Scott, L. (2002). Grassland development under glacial and interglacial conditions in southern Africa: review of pollen, phytolith and isotope evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology* **177,** 47-57.

Sifeddine, A., Martin, L., Turcq, B., Volkmer-Ribeiro, C., Soubiès, F., Cordeiro, R. C., and Suguio, K. (2001). Variations of the Amazonian rainforest environment: a sedimentological record covering 30,000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology* **168,** 221-235.

Silva, L. C. R., Sternberg, L., Haridasan, M., Hoffmann, W. A., Miralles-Wilhelm, F., and Franco, A. C. (2008). Expansion of gallery forests into central Brazilian savannas. *Global Change Biology* **14,** 2108-2118.

Sjogren, P., van Leeuwen, J. F. N., van der Knaap, W. O., and van der Borg, K. (2006). The effect of climate variability on pollen productivity, AD 1975-2000, recorded in a Sphagnum peat hummock. *The Holocene* **16,** 277-286.

Stace.C. (2004). Combretaceae. *In* "Flowering Plants of the Neotropics." (N. Smith, S. Mori, A, A. Henderson, D. W. Stevenson, and S. V. Heald, Eds.), pp. 110-113. Princeton University Press, Oxford.

Stockmarr, J. (1971). Tablets with spores used in absolute pollen analysis. *Pollen et spores* **13,** 615-621.

Sugita, S. (1993). A model of pollen source area for an entire lake surface. *Quaternary Research* **39,** 239-244.

Systat Software (2008). "SigmaPlot for Windows Version 11".

ter Braak, C. F. J. (1995). Ordination. *In* "Data Analysis in Landscape and Community Ecology." (R. H. G. Jongman, C. F. J. ter Braak, and O. F. R. Van Tongeren, Eds.). Cambridge University Press, Cambridge.

ter Steege, H., Pitman, N. C. A., Phillips, O. L., Chave, J., Sabatier, D., Duque, A., Molino, J.-F., Prevost, M.-F., Spichiger, R., Castellanos, H., von Hildebrand, P., and Vasquez, R. (2006). Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* **443,** 444-447.

Thomas, W. W. (2004). Cyperaceae. *In* "Flowering Plants of the Neotropics." (N. Smith, S. Mori, A, A. Henderson, D. W. Stevenson, and S. V. Heald, Eds.), pp. 434-436. Princeton University Press, Oxford.

TROPICOS.org. Missouri Botanical Garden. Accessed 29 Aug 2008 <http://www.tropicos.org>

van der Hammen, T. (1974). The Pleistocene changes of vegetation and climate in Tropical South America. *Journal of Biogeography* **1,** 3-26.

van der Hammen, T., and Hooghiemstra, H. (2000). Neogene and Quaternary history of vegetation, climate, and plant diversity in Amazonia. *Quaternary Science Reviews* **19,** 725-742.

van Tongeren, O. F. R. (1995). Cluster analysis. *In* "Data Analysis in Community and Landscape Ecology." (R. H. G. Jongman, C. F. J. Ter Braak, and O. F. R. Van Tongeren, Eds.), pp. 174-212. University of Cambridge Press, Cambridge.

Vélez, M. I., Berrío, J. C., Hooghiemstra, H., Metcalfe, S., and Marchant, R. (2005).

Palaeoenvironmental changes during the last ca. 8590 calibrated yr (7800 radiocarbon yr) in the dry forest ecosystem of the Patía Valley, Southern Colombian Andes: a multiproxy approach. *Palaeogeography, Palaeoclimatology, Palaeoecology* **216,** 279-302.

Webster, G. (2004). Euphorbiaceae. *In* "Flowering Plants of the Neotropics." (N. Smith, S. Mori, A, A. Henderson, D. W. Stevenson, and S. V. Heald, Eds.), pp. 146-150. Princeton University Press, Oxford.

Weng, C., Bush, M. B., Curtis, J. H., Kolata, A. L., Dillehay, T. D., and Binford, M. W. (2006). Deglaciation and Holocene climate change in the western Peruvian Andes. *Quaternary Research* **66,** 87-96.

Weng, C. Y., Bush, M. B., and Silman, M. R. (2004). An analysis of modern pollen rain on an elevational gradient in southern Peru. *Journal of Tropical Ecology* **20,** 113-124.

Wooller, M. J., and Beuning, K. R. (2002). Introduction to the reconstruction and modeling of grass-dominated ecosystems. *Palaeogeography, Palaeoclimatology, Palaeoecology* **177,** 1-3.

Wright, H. E., Jr., McAndrews, J. H., and Zeist, W. v. (1967). Modern pollen rain in Western Iran, and its relation to plant geography and Quaternary vegetational history. *The Journal of Ecology* **55,** 415-443.